The Journal of HEREDITY

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The Early Days of Genetics

"Somatic Reduction": Its Causes and Significance

Genetic Effects of Cosmic Rays and Thermal Neutrons

VOLUME 42 JULY-AUGUST, 1951 NUMBER 4

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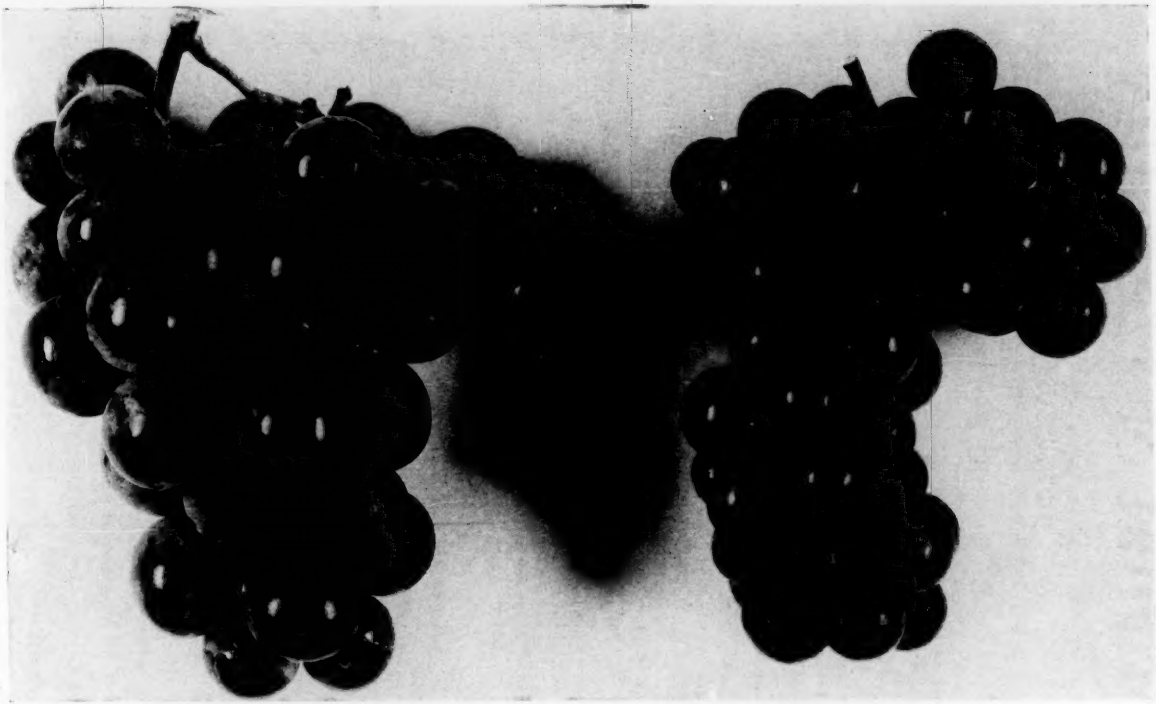


LARGE BERRIED SPORT OF FREDONIA GRAPE

Figure 1

Both these bunches of grapes are from the same vine. The cluster on the left was picked from a cane that produced only large berried fruit. The cluster on the right is typical of the variety and was borne on a normal cane.

CHIMERAL SPORTS OF GRAPES*

Alleged Tetraploid Varieties Have Diploid "Skin"

JOHN EINSET AND BARBARA LAMB

NEBEL reported[7] the earliest chromosome counts of large-berried or "gigas" sports of grapes in 1929. These sports of the varieties Sultanina and Muscat of Alexandria were reported to have 76 chromosomes or twice the normal diploid number of 38. More recently Olmo in California has published several papers dealing with "Giant" berried or tetraploid grapes. He has shown that several commercial grape varieties are tetraploids and has described them as large-berried sports of existing diploid varieties. The Muscat Cannon Hall which is grown in England under glass was reported[8] in 1937 to be a tetraploid Muscat of Alexandria. The Pierce or California Concord was found to be a tetraploid Isabella and four different varieties from Japan were found to be tetraploid forms of Campbell Early, Catawba, Delaware and Niagara.[9]

Other large sports have also been described as tetraploids by workers in other grape regions of the world.[3,10]

The writers have previously reported and described a number of spontaneous large-fruited bud sports of apple.[4,5] These sports were found to be periclinal chimeras in which the periclines differed in chromosome number. All the sports had a "skin" of diploid cells overlying the tetraploid internal tissues. Three types were described that differed in the relative numbers and locations of diploid (34 chromosome) cells and tetraploid (68 chromosome) cells. The simplest condition prevailed at the stem tips where in different sports one, two or three diploid cell layers covered the internal tetraploid tissue. The distribution of diploid and tetraploid cells in the stems, leaves and flowers of the various sports has been described in detail.[1,2]

In view of the chimeral structure of all of the fifteen or more apple sports that have been investigated it would seem likely that the grape sports, too, might be diploid - tetraploid chimeras, rather than wholly tetraploid in their makeup.

Cytological Studies

The Eaton is a Concord-type grape described as a "pure-bred" seedling of Concord originating in 1868 from seed of Concord.[6] Our evidence indicates that it must be a large-berried sport of the Concord or of a grape of this type. The Eaton was considered to be a tetraploid as determined by chromosome counts made in root-tips from rooted cuttings. The breeding behavior of this grape also demonstrated its apparent tetraploid nature. Upon self-pollination it produced tetraploid seedlings and when crossed with diploid varieties it produced triploid seedlings.

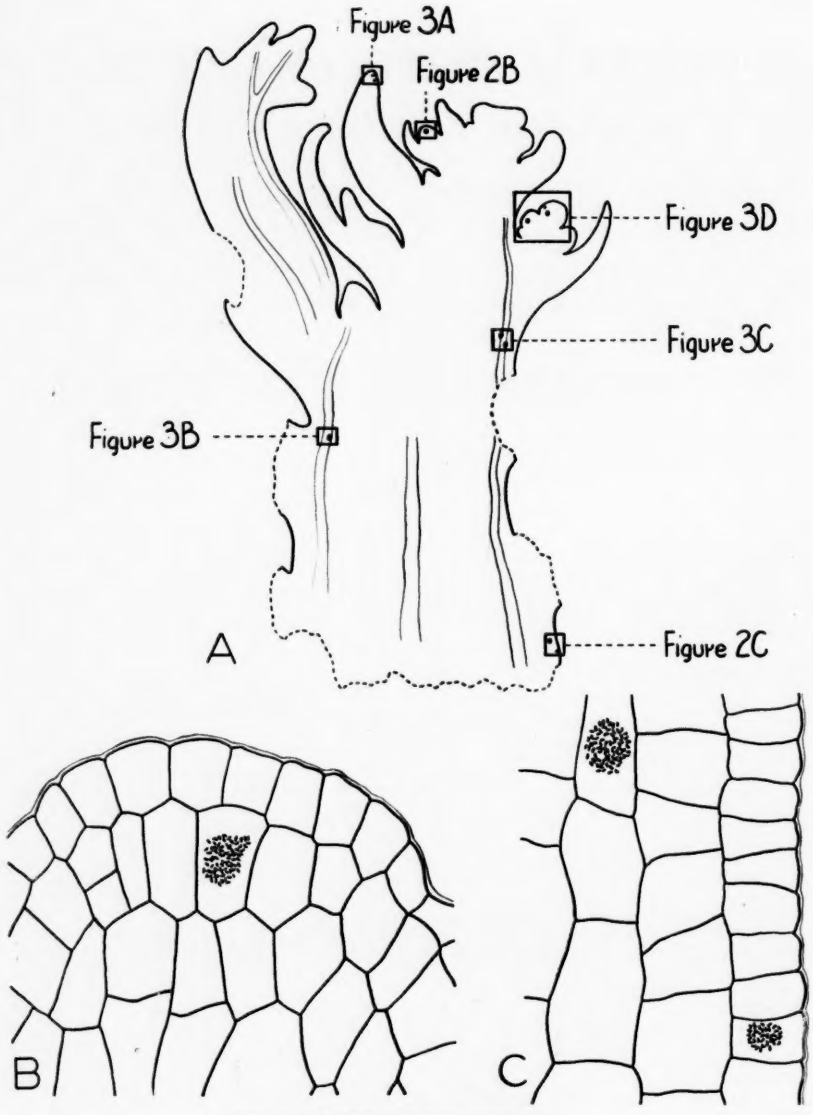
However, sections of rapidly growing buds full of dividing cells have revealed the true chromosomal nature of the Eaton grape. Most of the cells are tetraploid with 76 chromosomes but the epidermal cells are diploid with 38 chromosomes. This was true in every instance where the chromosome number of a cell could be determined with certainty.

Preliminary studies have been made of several other large berried sports that have been sent in to the Station. Most of these have been of the Concord and Fredonia varieties. Chromosome counts in root tips have given the tetraploid number but examination of buds has shown in each instance that the epidermal layer has been diploid. In some of the sports diploid cells have also been found in deeper tissues.

Conclusion

In studies of chromosome numbers of grape varieties and sports, counts have apparently in most instances been made in root-tips of rooted cuttings. Roots arise in inner tissues of a cutting and in the varieties reported to be tetraploid the tissues of root origin were undoubtedly tetraploid. Some chromosome determinations have also been made in root-tips of seedlings of the varieties being investigated. Chimeras of the same type as the Eaton behave like tetraploids when used in crosses. Chimeras with a thicker diploid outer layer might behave like diploids as they do in the apple sports. For this reason chromosome numbers of seedlings may be misleading as to

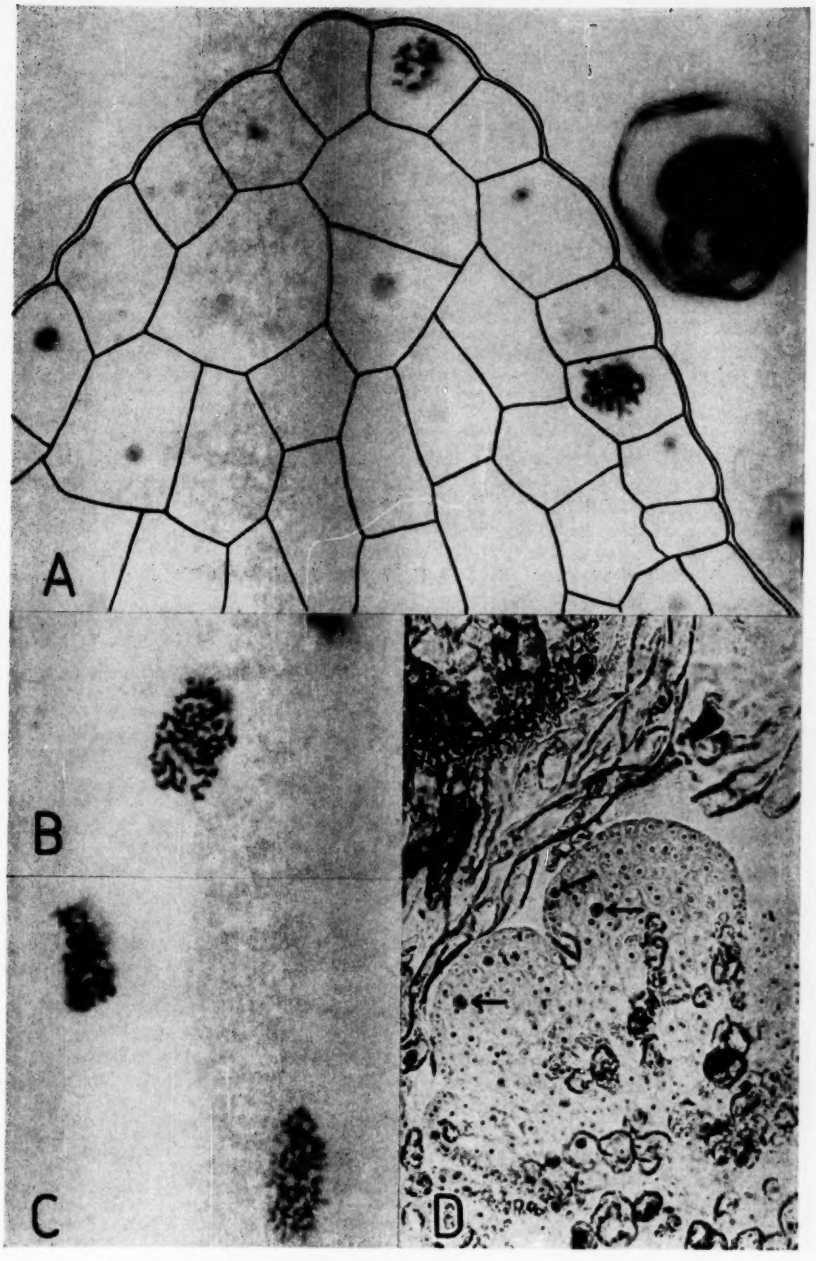
*Approved by the Director of the New York State Agricultural Experiment Station for publication as Journal Paper No. 861.



DIPLOID-TETRAPLOID CHIMERAS

Figure 2

A—Longitudinal section of a bud of the Eaton grape showing locations of the various sketches and photographs. The bud scales and older leaves have been dissected off. *B*—Section of lateral bud showing a sub-epidermal cell with the tetraploid number of 76 chromosomes. *C*—Section of stem with an epidermal cell containing the diploid chromosome complement and a cell in the third layer with the tetraploid chromosome complement. (magnification about 2500 ×).



THE CHROMOSOMES OF THE EATON GRAPE

Figure 3

A—Longitudinal section of a young leaf showing epidermal cells with the diploid complement of 38 chromosomes. *B* and *C*—Cells in vascular tissue of the stem showing the tetraploid chromosome complement. *D*—Section of a cluster primordium. Note the diploid epidermal cell and two tetraploid inner cells. (magnification of *A*, *B* and *C* about 2500×).

the chromosome constitution of the parent.

In view of the structure and behavior of "Giant" apple sports and the similarity in structure of the examined grape sports it appears likely that many, perhaps all of the tetraploid grapes are diploid-tetraploid periclinal chimeras rather than wholly tetraploid forms.

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A METHOD FOR TESTING TWO-FACTOR INHERITANCE

D. C. Rife

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SIMPLE modes of inheritance involving only two or more allelic genes may be readily checked by gene frequency analysis, providing the population is in genetic equilibrium. Gene frequencies cannot be easily calculated for modes of inheritance involving two or more pairs of factors, which are cumulative and equal in their effects. But it is possible to check the mode of inheritance by a comparison of phenotypic ratios, where only two pairs of factors are postulated.

Davenport proposed two pairs of factors, equal and cumulative in their effects, to be responsible for differences in the pigmentation of Negroes and Whites. I shall use his hypothesis to illustrate the derivation and application of a formula for testing this type of inheritance. The phenotypes and genotypes of various shades of skin color, according to this scheme, are as follows:

Genotypes	*Phenotypes*
SSTT	black
SsTT, *SSTt*	mulatto
SStt, *ssTT*, *SsTt*	dark brown
Sstt, *ssTt*	light brown
sstt	white

Allow: p = frequency gene *S*
q = frequency gene *s*
u = frequency gene *T*
v = frequency gene *t*

If the population is in equilibrium the genotypic frequencies may be readily calculated and illustrated as shown below.

	p^2	2pq	q^2
u^2	black p^2u^2	dark brown $2pqu^2$	mulatto q^2u^2
2uv	dark brown $2p^2uv$	mulatto 4pquv	light brown $2q^2uv$
v^2	mulatto p^2v^2	light brown $2pqv^2$	white q^2v^2

$$\begin{aligned}
\text{black} &= p^2u^2 \\
\text{dark brown} &= 2p^2uv + 2pqu^2 \\
&= pu(2pv + 2qu) \\
\text{mulatto} &= q^2u^2 + 4pquv + p^2v^2 \\
\text{light brown} &= 2pqv^2 + 2q^2uv \\
&= pv(2pv + 2qu) \\
\text{white} &= q^2v^2
\end{aligned}$$

It follows that the dark brown $= \sqrt{\text{black}} \times (2pv + 2qu)$

light brown $= \sqrt{\text{white}} \times (2pv + 2qu)$

$$\text{Therefore } \frac{\sqrt{\text{black}}}{\sqrt{\text{white}}} = \frac{\text{dark brown}}{\text{light brown}}$$

This type of analysis is easily performed. One need only to determine phenotypic ratios from a population which is in equilibrium. Unfortunately most mixed populations are not in equilibrium with respect to skin color. The same test may of course be applied to any trait whose inheritance is suspected to be controlled by two independent pairs of alleles, equal and cumulative in their effects.

THE REDISCOVERY OF GREGOR MENDEL'S WORK

An Historical Retrospect*

ERICH VON TSCHERMAK-SEYSENEGG
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The last surviving re-discoverer of Mendel's research in the genetics of the garden pea will celebrate his eightieth birthday on November 15, 1951. It is a privilege to be able to present Professor von Tschermak's recollections of the birth pangs of genetics and of the early infancy of the science of heredity a half century ago. We speak surely for the Geneticists in all countries in extending to this Nestor of our science greetings and all good wishes on this notable occasion.—*Editor*

IT was the fate of Gregor Mendel's name to be known by few during his life, to be almost forgotten for decades, but to be on the lips of all biologists today. Yet 85 years ago Mendel had recognized the reign of biological laws in the field of heredity and hybridization where superficial observation disclosed only apparent disorder and chance. With the discovery and proof of his laws of hybridization he actually created a fruitful field for the experimental approach to the inheritance of individual characteristics of organisms, to the biology of reproductive processes, and above all to practical plant and animal breeding. The development of this field, however, did not begin until after the rediscovery of Mendel's teachings in 1900. Although he could enjoy the inner pleasure and satisfaction accruing from his work, he was denied recognition and esteem, the tribute of the contemporary world due this magnificent conception. Mendel's posthumous fame has spread over all countries all the more brilliantly and rapidly. The omission of his period has been rectified by the present.

Today Mendel's theories are in a sense the cornerstone and foundation of an ever-expanding scientific structure. He is the symbol of a fertile direction in scientific and practical work, recognized as Mendelism by every biologist, by most physicians, farmers and breeders, even by the high school student. With patient work Mendel created the solid empirical basis of an exact science of heredity, which does not follow brilliant hypotheses, but necessitates rational experimentation. He did this at a time when the majority of botanists and zoologists had succumbed to the temptation of finishing prematurely the speculative structure of plant and animal heredity, the "dangerous" testing of which followed much later. In view of these circumstances it is not surprising that Mendel's program, ahead of its time, even modern today, remained at first but poorly understood, his example unfollowed. The genial man had at least sensed the scope of his theory, nonetheless he looked forward, without impatience and rancor, with rare modesty and equanimity, to the time when the planted seed must inevitably come to flower and fruit.

Retrospect

In view of the importance which Mendelism has now attained it is quite natural to have a look back from time to time to the birth of this new, relatively young science termed genetics. Fifty years have passed since Gregor Mendel's work was rediscovered and fully recognized. As the only living one of the three rediscoverers of Mendel's work it becomes

*This article is a translation of a lecture which Professor von Tschermak-Seysenegg gave on the occasion of the celebration of the 100th anniversary of the founding of the Zoologisch-Botanischen Gesellschaft in Wien in June, 1950. At that time the author was awarded an honorary doctorate of science by the University of Wien. The lecture was published in 1951 in Volume 92 of the *Verhandlungen der Zoologisch-Botanischen Gesellschaft.*

my privilege to take this historical glance back to the time of rediscovery. I have reported elsewhere ("Wien, der Ausgangsort des praktischen Mendelismus," *Zeitschr. für Pflanzenzüchtung* 29:262-275, 1951) on the joys and sorrows of the early application of Mendelism at the Institute for Agriculture in Vienna and at numerous agricultural establishments in Austria. As is the case with almost all fundamental discoveries, Mendel had a number of predecessors. I shall mention here the names of only those scientists and breeders who, through their experiments, actually approached the Mendelian laws of inheritance. I shall refer primarily to the book *Plant Hybridization Before Mendel,* by my deceased American friend, Professor H. F. Roberts, published in Princeton in 1929.

John Goss reported to the London Horticultural Society in 1824 on the sole expression of yellow seed-color in the first generation after hybridization of a blue-green seeded pea with a yellow one, followed by yellow and green seeds in the second seed generation, subsequent constancy of a portion of the yellows and continued segregation of the remainder of the yellow offspring, and a continued constancy of the greens. He had already found the fact of the dominance of yellow over green, the law of dominance and uniformity, as well as the variation or segregation, in modern terminology, in the second seed generation. He could not penetrate to the mathematical regularity of segregation because he did not follow individual plants in harvesting and planting. Analogously, somewhat later than Mendel, Laxton observed dominance of smooth seeds, red blossoms and pigmented seed coats in the F_1, segregation in the F_2 of his pea crosses. Darwin as well carried out pea crosses and obtained xenia and in some cases heterosis.

The Frenchman Sageret (1826), in his crosses with melons, came closest to the idea of the independent inheritance of parental characteristics. He found that the appearance of the hybrids could not be explained by a blending of parental characteristics, but rather by a distribution of these characters *per se* and their various combinations in different members of the progenies.

Naudin (1863) observed in his hybrids a great F_1 uniformity and regarded the hybrid as a living mosaic in which the various elements are so completely blended that the eye cannot differentiate between them. The separation of parental inheritance materials becomes complete during the formation of sex cells. "Both the pollen cells and primordial seed cells contain in part only the paternal, in part only the maternal essence." Chance determines the number of F_2 forms. Naudin approached the truth but went past it.

The Nägeli Episode

One who cannot be spared the blame for the circumstance that Mendelism was not already initiated in 1867 is the famous botanist Carl Nägeli, then Professor in Munich. He was not only well informed on Mendel's work but had his pea material at hand. In the event of immediate recognition, of course, we would hardly be speaking of Mendelism today; his fame would not have attained such proportions. We owe to Correns the publication of the entire, highly interesting correspondence which Mendel initiated with Nägeli with a letter on New Year's Eve 1866, accompanying Mendel's reprint. This correspondence lasted until 1873. These letters show, as we know today, that Mendel published only a fraction of his experiments and, in addition to his pea work, had set up hybridization experiments with 16 other plant species. We must regret today that Mendel reported in his first letter recent crossing experiments with different Hieracium species and asked for Nägeli's help in these studies, since he knew that Nägeli was occupied at this particular time with Hieracium studies, as the speciation question had become of immediate importance through Darwin's writings.

We also know Nägeli's answer to this [first] letter, following two months later, since a fragment of it remained pre-

served in the cloister in Brünn and was given to Mendel's biographer, Iltis. In the first part of the letter Nägeli criticized—one must say somewhat condescendingly—Mendel's pea experiment by writing: "It appears to me that the experiments with Pisum are not completed but that they should really just begin"; a severe imposition if one considers that Mendel's paper was based on observation of over 10,000 hybrids and 355 artificial pollinations and reported on the perfectly clear results of his completed experimental groups. It would have been more justified to ask Mendel to publish his experiments in detail as is the custom of most workers today. On the other hand, it is the very brevity and conciseness of Mendel's work, perhaps an expression of his excessive modesty, which impresses us particularly. Nonetheless, Nägeli asks Mendel in his only letter dealing with the Mendelian pea work for seed of his hybrid forms. The conclusion of the letter shows Nägeli's pleasure in finding in Mendel a competent experimenter and useful collaborator for his Hieracium work.

Despite the somewhat haughty criticism of Nägeli, who, after all, considered Mendel an amateur and apparently did not fully grasp his significant conclusions, the modest Mendel, happy with the receipt of several of Nägeli's reprints, answered fully and defended the constancy of hereditary characteristics in his pea hybrids which he had followed for 4-5 generations, but was nonetheless doubted by Nägeli. Concurrently Mendel sent no less than 140 labelled seed packages and gave the method by which the seeds or the resulting plants could be tested as to their hereditary traits; he also suggested experiments which should prove his idea of the purity of gametes, that is, his sentence that "the hybrids form as many egg and pollen cells as there are possible constant combinations." Although Nägeli had some of these seeds planted in the spring of 1867, no confirmative tests were begun; nor is there any mention of Mendel's pea work in further letters addressed to Mendel. On the other hand, there is considerable discussion later of Hieracium and its hybrids, which were also mutually exchanged.

The correspondence stopped in 1874; the hard battle of Mendel over the ruinous cloister tax had begun and had paralyzed Mendel's hybridization experiments. It is yet little known that the botanist Herman Hoffmann of Giessen had read Mendel's Pisum article. Citing it in his own work, *Untersuchungen des Wertes von Spezies and Varietät, ein Beitrag zur Kritik der Darwinschen Hypothese,* [Evaluation of species and variety, a contribution to the criticism of Darwin's hypothesis], he gathered from it only "that the hybrids have the tendency, in later generations, to revert to the parental species." (The same view, incidentally, was also held by two outstanding botanists soon after the rediscovery of Mendel's laws, an indication of the lack of thoroughness with which they had read the first papers of the three rediscoverers of Mendel.) Hoffmann reported also on some of his own bean and Hieracium crosses without acknowledging Mendel in that connection. To the Viennese botanist Kerner, Mendel had also sent one of his 40 reprints with an accompanying letter. It appears that he did not read the paper; the pages of the reprint were not even cut. He, too, was probably more interested in the Hieracium hybrids of Mendel; we do know that he had obtained some of Mendel's Hieracium plants through his friend Professor v. Niessel in Brünn.

Contemporary Work

In the realm of agricultural plant breeding there were later two men who, but a few years before the rediscovery, came close to finding a numerical relationship in the regular segregation behavior in their crosses of cereals and leguminosae, namely the well-known German plant breeder, Dr. Wilhelm Rimpau in Langenstein and the Swede, Pehr Bohlin in Svalöf. Rimpau, in his numerous hybridizations of cereal races, had made valuable notes on the domination of some characters as well as on the uni-

formity of the first hybrid generation, and had clearly recognized the constancy of some characteristics, for example the bearding in wheat after crossing bearded wheat forms with beardless ones, the 4-rowedness in crosses between 2-rowed and 4-rowed barleys. From the notations in his book *Kreuzungsprodukte landw. Kulturpflanzen* [Hybridization Products of Agricultural Plants] in the Agric. Yearbook 1891, I could in 1901 already see the dominance and recessivity of numerous characteristics and utilize these in my first evaluation tables for cereals. He cited Focke's book *Pflanzenmischlinge 1881* [Plant Hybrids, 1881] in describing his pea crosses, quoting at times whole sections; it is quite surprising that he did not notice Mendel's citation in Focke.

In the book, *Svalöf 1886-1946*, Prof. Dr. Åkerman states that Pehr Bohlin and Hans Tedin had already carried out crossing experiments between different varieties of barley, peas, and sweetpeas before the end of the last century, that Bohlin reported on their results at the Agricultural Congress in Stockholm in 1897. He stated at the time "that in the F_1 there was no variation while the forms appearing in the F_2 and subsequent generations represented all possible combinations of the parental characteristics and could be predicted with almost mathematical accuracy." Bohlin was thus even closer than Rimpau to rediscovering the Mendelian laws, a fact which has not been shown in the pre-Mendelian literature. Millardet's strawberry hybrids 1894, his so-called faux hybrides [false hybrids] resemble Mendel's Hieracium hybrids closely, differing only in that the behavior which occurs only occasionally and with a few characteristics in the latter is the rule in the former. The hybrid shows either the characteristics of the father or those of the mother, that is, all those of one or the other parent, so that it would not be recognized as a hybrid were its derivation not known.

On the zoological side, the experimental crosses between mottled Japanese dancing mice and normal whites of W. Haacke must be mentioned; he reported on these in 1893 in his book *Gestaltung und Vererbung* [Form and Inheritance]. That Haacke was not able to state a universal rule was due on the one hand to his experimental methods which treated a whole generation summarily and not each individual as such, and on the other to his complex theoretical conceptions. Neither Haacke nor Guaita, who began crossing mice some years later, knew of Mendel's work; otherwise their experiments would have led them further.

We see, then, that in the case of all the above botanical and zoological crossing experiments there was missing that deep penetration into the material which Mendel achieved through the sharp separation of the species character into the individual characteristics, the systematic character analysis, and especially through his regard for the numerical relationships of the segregation products in the various generations of his hybrids.

To the conscientious collecting of W. Olbers Focke (died 1922) we are indebted finally for a short discussion of Mendel's pea experiments and the announcement of the appearance of his paper, while he also turned with more attention to the Hieracium hybrids and especially to the hybrid between *Phaseolus vulgaris* and *Ph. multiflorus,* in his widely read book *Pflanzenmischlinge 1881* [Plant Hybrids 1881]. He stated only that Mendel's numerous pea crosses "gave results which were quite similar to those of the plant physiologist Knight, but that Mendel believed to find constant numerical relationships among the hybrid types." That was all that struck him in Mendel's pea work which, it must be admitted, came into his hands only shortly before the completion of his book. It was probably Hoffmann's citation of Mendel which brought the latter's work to his attention, since Nägeli, in his treatise *Mechanisch-physiologische Theorie der Abstammungslehre* [Mechano-physiological theory of heredity], appearing in the year of Mendel's death, did not even mention the apparently forgotton experiments of

Mendel which, incidentally, would have furnished considerable support for a great number of his observations and concepts.

Mendel had not sent his paper to Darwin. "To him more than all others," states Bateson, "the news of an advance in the problem whose solvability he was first to show to the world, would have been a sincere pleasure, even though the direction taken by this advance was other than that which he himself expected."

The Re-Discovery

Thus a whole group of workers came stepwise ever closer to a regularity in the inheritance of characteristics in plants and animals, until finally three botanists, Hugo de Vries, C. Correns, and myself, simultaneously and independently, and without knowledge of Mendel's work, succeeded in 1900 in discovering numerically calculable combination in the progeny of hybrids, and could finally celebrate the resurrection of Mendel's work in reading its citation by Focke.

All three scientists had proceeded from individual questions on the problem of fertilization. Yet how different were their ways even from the beginning. De Vries was particularly absorbed in concepts of descendence theory; his major problem remained the mutation question, while to him, though one of the rediscoverers of Mendel, the application of the hybrid regularities to practical plant breeding was of less interest. As early as 1898 he noted in the results of the cross *Oenothera Lamarckiana* and *Oe. brevistylis* the dominance of one of the two antagonistic properties, the uniformity of the F_1, the separation, segregation, of these two properties in the formation of pollen and egg cells in a 3:1 ratio; he found the same confirmed later in 16 other hybrids.

Only at this time did he thoroughly read the book *Plant Hybridization* sent to him by Prof. Bailey in 1892 and found there Focke's citation of Mendel, obtained Mendel's paper and was very surprised to find the same regularities already described and explained in detail by Mendel. De Vries could actually have published some of his results prior to 1900. His first short communication *Sur la loi de disjonction des hybrides* [On the Law of Disjunction of Hybrids] appeared on March 26th in *Comptes Rendus* and contains, without mentioning Mendel's name, the terms "dominant" and "recessive"; through this circumstance Correns and I, who were just about to report on our experiments, became aware of the fact that de Vries must have known of Mendel's work.

In the March issue of the *Berichte der Deutschen Botanischen Gesellschaft* appeared a preliminary but detailed communication from de Vries, *"das Spaltungsgesetz der Bastarde"* [The Law of Segregation of Hybrids], which reported at some length on the agreement between his results and those of Mendel. From then on de Vries' interest once more belonged to his mutation problem. He soon left the front ranks of experimenters in heredity. Only later, when the research in heredity approached the solution of the problems of descent did he return to a consideration of Mendelism.

It is interesting to note that de Vries apparently became quite jealous of the rapid development of Mendelism, and considered his mutation theory somewhat ignored, especially among breeders. Only such a jealousy can explain the fact that he did not even mention Mendel's name in his 1907 book *"Pflanzenzüchtung"* [Plant Breeding] and his brusque refusal to sign a petition for the erection of a Mendel memorial in Brűnn in 1908.

Correns proceeded in his heredity research from the problem of fertilization. Even before the explanation of double fertilization he was interested in xenia, leading him to crosses with maize and peas, and to the discovery of a regularity in counting the segregation products. He had already read the chapter on xenia in Focke's book, where the name of Mendel is not mentioned; only later, while studying the discussion of pea hybrids in Focke's book, did he notice the Mendel citation, prompting him to ob-

tain Mendel's paper. There he, like de Vries, saw that he had a predecessor.

Correns had begun his pea crosses four years before his first Mendel publication. In October, 1899, he found, as he states, the explanation for the 3:1 segregation ratio suddenly, like lightning, after a sleepless night. He also reported even then that in addition to dominance there is an intermediate inheritance, and the existence of coupled characteristics as well as independent ones.

On April 21st, 1900, Correns received a reprint of de Vries' short essay *Sur la loi de disjonction des hybrides*. This led him to send his almost completed report, *Gregor Mendel's Regel über das Verhalten der Nachkommenshaften der Bastarde* [Gregor Mendel's rule on the behavior of the progenies of hybrids] on April 22nd to the editors of the *Berichte der Deutschen Botanischen Gesellschaft*. It was presented at the April 27th meeting and appeared in the May issue. Correns remained throughout his life the famous fundamental scientist of the science of heredity, who was particularly interested in the inheritance of sex but less so in practical questions. He was the first to give the designation Mendelian Laws to Mendel's crossing results.

The Author's Experience

It will probably not be considered presumptuous of me, the last living of the three rediscoverers of Mendel, that I, on the occasion of the Mendel Festival at the Institute for Agriculture in Vienna in July, 1950, reported on the history of my crossing experiments in Gent, on their continuation in Vienna, as well as on the surprises and disappointments, at least in the first moment, caused by the finding of Mendel's paper and the papers of de Vries and Correns which appeared but a few months and weeks before.

In my two years' stay at well-known seed farms in Stendal and Quedlinburg and in my visits with the old master of German cereal breeding, Dr. Wilhelm Rimpau, I was particularly interested in the crosses carried out there among cereals and flowers; I lectured on these before the Agriculturist & Silviculturist Club in Vienna. On this occasion the then present Prof. v. Liebenberg, of the Institute for Agriculture, promised me the position of teaching assistant in the near future. A student of my father's, the mineralogist Prof. Renard of the University of Gent, recommended for my further training a stay at famous centers of flower and fruit—particularly grape — breeding situated near Gent. Since this was not sufficient to occupy my time I asked the famous flower biologist, Prof. MacLeod, Director of the Gent Botanical Garden, for permission to begin crossing experiments at the Botanical Garden, designed primarily to study the growth-stimulating effect of foreign pollen described by Darwin in his book, *On the Effect of Cross and Self-pollination in the Plant Kingdom*, as well as the xenia problem in peas. I also began at that time to carry out crosses between various leguminosae genera, for example, pea × lentil × sweetpea (Lathyrus) which, repeated many years later, led to the discovery of artificially induced parthenogenetic seed development. As I planned to become acquainted with the establishment of Vilmorin in Verriere, near Paris, during July and August, I asked the gardener at the Botanical Institute in Gent to harvest and send to Vienna the seed of my crosses. Fortunately this shipment reached my hands safely, although it was not even registered.

The promised assistantship was still not vacant in 1899 and Prof. v. Liebenberg recommended my spending a year at one of the imperial family estates in Esslingen, near Gross-Enzersdorf, since an experiment station of the Institute was to be founded there with the promise of a position for me. Nonetheless, I spent the major part of my time in the private garden of a Viennese banker who permitted me to continue my pea crosses in pots on home-made benches and in a larger garden plot. There I began some experimental crosses with beans and various flowers. In 1900 I

was able to continue my plantings in a plot in the garden of the Institute. In studying the results of my pea crosses in the fall of 1899 I discovered the 3:1 segregation ratio for yellow and green cotyledons and smooth and wrinkled seeds, as well as the 1:1 ratio in backcrossing the green cotyledon peas with hybrid pollen, in the second seed generation of all of my experimental groups.

While recording these results I saw the citation of Mendel in Focke's book and obtained from the University library the volume of the *Naturforschender Verein in Brünn* containing Mendel's paper. There I read to my great surprise that Mendel had already carried out such experiments much more extensive than mine, had noted the same regularities, and had already given the explanation for the 3:1 segregation ratio. This was the first surprise I encountered in the preparation of my *Habilitationsschrift** which I hurried to completion in order to hand it to the editors of our Institute on January 17th, 1900.

In March, de Vries and, as already mentioned, Prof. Correns, sent me his [de Vries'] short discussion from *Comptes Rendus*, containing not the name of Mendel but the designations "dominant" and "recessive" coined by him [Mendel]. That was sufficient to convince me that de Vries knew the Mendel paper and had utilized it in his own crossing experiments. Naturally, I hurried to the editor's office on the same day in order to obtain the already corrected *Habilitationsschrift* for immediate publication. Who would publish this paper with its numerous tables? It was much too extensive for the *Berichte der Deutschen Botanischen Gesellschaft* and I too poorly informed to know who could accept the paper. Fortunately my friend Dr. Bersch, then editor of the *Zeitschrift für das landw. Versuchswesen* in Österreich, was willing to accept the work with the promise of immediate publication.

In the meantime the detailed paper of de Vries with reference to Mendel's work, *Das Spaltungsgesetz der Bastarde*, appeared in the March issue of the *Berichte der Deutschen Botanischen Gesellschaft*. While going through the second correction of my own paper, there appeared, I may say to my horror, the paper of Correns, *Gregor Mendels Regel über das Verhalten der Nachkommenschaft der Bastarde*, in late May. It was now high time for me to come out with my part in the rediscovery of Mendel's laws. I therefore prepared an abstract of my extensive paper immediately for the June issue of the *Berichte der Deutschen Botanischen Gesellschaft*. I was also able to send reprints of my paper *Über Kreuzung von Pisum sativum"* [On artificial crossing in *Pisum sativum*] from the *Zeitschrift für das landw. Versuchswesen* to de Vries and Correns but a few days before, in order to be able to prove my simultaneous rediscovery.

A fight over priority could not and did not come about, despite the fact that de Vries and Correns, by virtue of the earlier beginning of their hybridization experiments, could report on more extensive experimental material. Aside from a minor skirmish between myself and Correns at the Naturalists' meeting in Meran, in 1903 no scientific disputes developed. There I reported on my theory of kryptomery and kryptohybridity to which Correns could furnish some contributions but on which by chance he could not report until a day later. A frank discussion on the occasion of this meeting led to mutual recognition and evalution of the different fields of endeavor.

A few of Correns' and Fritz Wettstein's students thought in later years to have found a certain gradation in merit with respect to the recognition of the significance of Mendel's laws for the problems of modern biology and therefore the initiation of the modern science of heredity. This prompted me, finally, to write a short contradiction in the periodical *Der Züchter* in 1937. It was, after all, not easy for the young Tscher-

*An academic qualifying paper on extensive post-doctoral research.

mak to assert himself with his share of the find and his practical breeding application of Mendelism, since the then leading textbooks of R. v. Wettstein and Strasburger mentioned only the names of de Vries and Correns. This mistake was rectified in the succeeding editions.

How highly I valued the importance of the Mendelian laws for biology already in 1900 I have shown by requesting the inclusion and publication of Mendel's papers in Ostwald's *Klassiker der exakten Wissenshaft* [Ostwald's classicists of exact science] in the year of rediscovery. The three rediscoverers were fully aware of the fact that the independent discovery of the laws of heredity in 1900 was far from being the accomplishment it had been in Mendel's time since it was made considerably easier by the work which appeared in the interval, especially the cytological researches of Hertwig and Strasburger. Consequently the three rediscoverers were less interested in being celebrated as rediscoverers of rules they themselves designated "Mendel's laws," than in the successful utilization of these laws for the development of their various fields: de Vries for the mutation theory, Correns for fundamental research in inheritance, and I for practical plant breeding.

In the beginning the pioneers of Mendelism had to combat considerable resistance. The far-reaching importance of the discovery was denied or minimized. The leader of the English Mendelists, William Bateson, and his co-workers were opposed by the biometricians; in Sweden Nilsson-Ehle had a difficult time in converting the older so-called "high-breeders," and Johannsen succeeded only gradually in interesting the non-mathematically inclined majority of botanists in the elements of this precise science of inheritance. In Austria and Germany many pure botanists, so-called "unapplied" by Prof. Baur in contrast with the "applied" group, did not immediately grasp the meaning of combination breeding for their practical use. I cannot here enter into the details of the other pioneers of the new ideas and their experimental work.

Recollections of Mendel

A few words must be said about the two Mendel biographers, the high-school teacher Iltis and the botanist Oswald Richter, both active in Brünn. The former, in the year 1924, wrote a substantial book, *Gregor Johann Mendels Leben, Werk und Wirkung* [Gregor Johann Mendel's life, work and effect], the latter, in 1943, a book, *Gregor Mendel, die er wirklich war,* [Gregor Mendel as he actually was], implying that he disagreed with the biographical version of Iltis. Both biographers have earned considerable merit through their sincere efforts in collecting valuable biographical data from the Old Brünn cloister and from all localities where Mendel had worked as student, as teacher, as scientist, and as lecturer as well as data on his trips and on his scientific and social dealings.

In Vienna, in 1900, there were still two professors at our Institute for Agriculture, Profs. Friedrich and Liznar, who had been students of Mendel and could tell me some things about him. With Liznar he had been very friendly; he spoke with him about his meteorological observations on ground-water measurements, his bee experiments and his tax fight with the authorities. Only 14 days before his death he had written the following letter to Liznar: "Dearest friend! You have entered the years of ambition and creation, while almost the opposite is true with me. Thus I had to ask the directors today to relieve me of all meteorological arts since I can no longer read the meteorological instruments without assistance. Since we will hardly meet again in this connection may I bid you a hearty farewell and ask upon you all the blessings of the meteorological deities." Thus, shortly before his death, Mendel was still prone to mirth and could hardly be judged staid as Lenz had thought.

As is known, the so-called Mendel-Morganist genetics has been accused in recent years by a group of scientists of having contributed nothing for practical purposes. It is therefore very important

and timely that from Sweden, the country where the breeding of agricultural plants on a Mendelian basis has achieved the greatest practical successes, an outstanding geneticist, Prof. Arne Müntzing, pointed out unequivocally that Mendelism is "no theoretical plaything" but a science of the greatest importance for the national economy as well as for the public food supply.

Today, after 50 years, the Mendelian structure, whose foundations were laid twice and whose stories were solidly erected by the most renowned biologists of the world, stands proud and firm, armored against all attacks from the side of those geneticists who consider their illumination not inherited but acquired and would like to shake its walls by a mass of words. We do not stop our work for that, on the contrary, we are building on!

✦

A PROGENY TESTED CASE OF *HETEROCHROMIA IRIDIS* IN MAN*

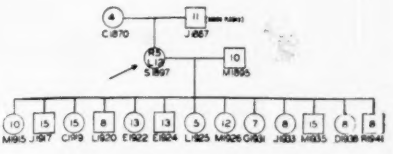
ISADORE LUDWIN

IN the course of a study of the heredity of Mediterranean Anemia, a woman was observed to have eyes of different colors—the right being brown and the left, blue. Further investigation disclosed that she was the mother of 13 living children, that her husband had distinctly blue eyes, and that both of her parents were alive. In addition, all members were available for examination and were most cooperative. These circumstances are sufficiently unusual to be worthy of note.

Eye color description by comparison with a standard was selected as an objective method of gathering data on eye color. The general eye color of the person examined was matched as closely as possible by daylight using the Augenfarben-Tafel† of Martin[1] as a standard. This eye color standard consists of a rectangular box containing 16 glass eyes ranging progressively from fully pigmented to very pale blue, numbered from 1 to 16 successively. For this study, categories 1-8 are considered brown and 9-16, blue.

The family pedigree is shown in Figure 4. II-1 is heterozygous for brown eye color since I-1, her mother, has brown eyes and I-2, her father, has blue eyes with brown flecks. No other case of mismatched eye color is known to exist among the relatives or descendants of II-1, the propositus.

The ratios expected from the backcross of a heterozygote to the double recessive, where a single autosomal gene with complete dominance is involved, were obtained. Seven of 13 children have eye color 9 or over, and six have eye color 8 or below. The fact that category 8 is genetically brown is demonstrated by the offspring of III-4, whose wife has distinctly blue eyes. Of their four children, three have blue eyes, while one has eyes unmistakably brown in color. (The family of III-4 is not shown in the pedigree.)



SOMATIC SEGREGATION IN EYE COLOR

Figure 4

The propositus (arrow) had a brown right eye and a blue left eye. Her thirteen living children had a perfect 1:1 backcross ratio. A color rating (numbers in symbols) of 1-8 indicates various shades of brown eyes; and of 9-16 indicates various shades of blue eyes.

One possibility for the origin of *Heterochromia Iridis* is that a point mutation in a somatic cell changed the gene controlling brown eye color. A different possibility is that the dominant gene was lost (as part of a lost chromosome) in an aberrant mitotic division. Both possibilities are considered somatic mutations.

The origin of *Heterochromia Iridis* in this woman is due to a somatic mutation.

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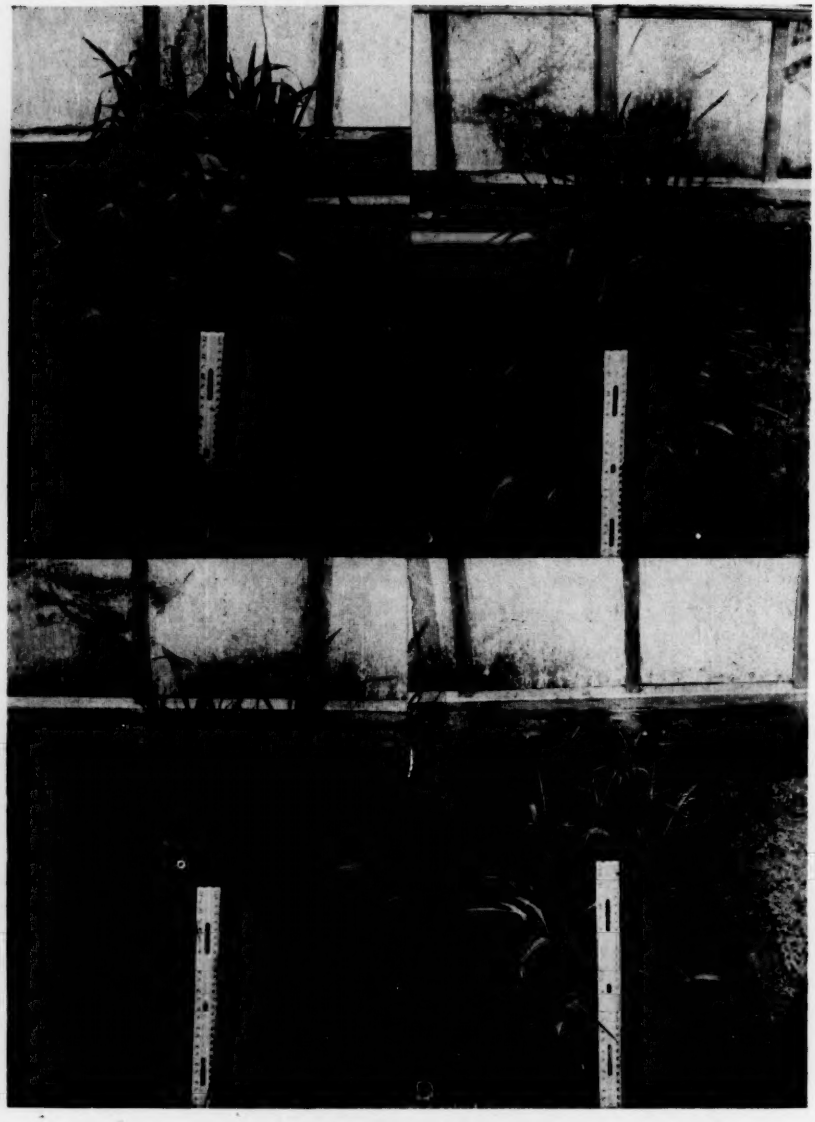
*Investigation performed while a Fellow of Tufts College.

†Augenfarben-Tafel of Martin made available through Dr. E. A. Hooten of the Harvard Museum of Comparative Anthropology.



THERMAL-NEUTRON EFFECTS

Figure 5

Thermal-neutron tolerance of maize kernals as indicated by plant height and leaf width of 34-day old seedlings. *A*—No treatment; *B-D*—Effects of progressively heavier dosages. *B*—2-minute exposure to thermal neutrons; *C*—4-minute exposure; *D*—8-minute exposure. Exposure to thermal neutrons had numerous effects on development. It reduced plant height and narrowed the leaves, but increased the leaf number. Many anomalies in color and form of leaves were also produced.

COMPARATIVE EFFECTS OF THERMAL NEUTRON IRRADIATION

Of Maize Pollen and Maize Seed on Subsequent Seedling Growth*

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THE rapid advancement in nuclear physics in recent years has made available the various products of nuclear fission for radiation experiments. The effects of the atomic bomb ionizing radiations on crop seeds have been reported by Anderson *et al.*[1] and Randolph *et al.*[12] for corn, by Brown[3] for cotton, and by Smith[13] for the cereals, barley, wheat, and oats.

While the atomic bomb is the most spectacular source of the various radiations, these same radiations can be produced by other means. In the past, extensive work on biological effects has been done with gamma rays from radioactive isotopes. Fast neutrons obtained from a cyclotron were used in radiation experiments by Lawrence and Lawrence[10] as early as 1935. However, since the thermal neutron flux available from cyclotrons is relatively low compared with that from a nuclear reactor, only a limited number of biological experiments have been performed with them. The atomic pile installations constructed during the past decade have given a readily-available source of fast and slow neutrons. These particles are of considerable interest in radiation experiments because they are uncharged, have high penetrability, and because of the high capture probabilities of nuclei of certain elements for these neutrons.

Thermal neutrons (energy less than 0.03 electron volts) as obtained from the heavy water pile of the Argonne National Laboratory, Chicago, Illinois, have been used by Frolik and Morris[6,7] in maize pollen irradiation work. Recently, Conger[4] and Conger and Giles[5] have reported on the cytogenetic effect of thermal neutrons on *Tradescantia* buds.

In maize irradiation experiments, both pollen and seed have been used extensively. It is the purpose of this paper to report the comparative effect of thermal neutron irradiation of maize pollen and maize seed as expressed by subsequent seedling growth.‡

Materials and Methods

The maize seed irradiated in this experiment was from a yellow dent F_1 single cross, L289 × 1205, the seed having been produced at Lincoln, Nebraska, in 1948. Corresponding seed carrying the effects of the pollen irradiations was produced at Naperville, Illinois, in 1948 by pollination of untreated plants of inbred L289 with irradiated pollen of 1205.

The pollen irradiations were made at the Argonne National Laboratory, Chicago, Illinois, on August 16, 1948, and the seed irradiations on May 17, 1949. The neutron irradiations consisted of exposures for various periods of time in the thermal-neutron column of a heavy water pile. Untreated material and one dosage of X-ray were included in each group for comparisons. The techniques of irradiating the pollen were the same as those previously described by Frolik and Morris.[7] The air-dry, dormant seed was paper packeted for the irradiation in the thermal-neutron column. The pile was operated at a power of approximately 250 kw. for the seed irradiations and at 300 kw. for the tassel samples. The neutron flux, 7×10^{10} neutrons/cm^2/sec.,

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†The work reported herein was done while the senior author was a Predoctorate Fellow in the Biological Sciences, the fellowship being provided by the Atomic Energy Commission and administered by the National Research Council.

‡More detailed information on these experiments, together with results of barley seed irradiation studies, are being reported in *Nebr. Agr. Exp. Sta. Res. Bul. 167*

was approximately the same for the two irradiations because the seed samples were placed closer to the pile proper. No shielding was employed in either case. The equipment and method of X-raying the pollen and seed were the same except for dosage, which was 1200 *r* units for the pollen and 7500 *r* units for the seed, and the fact that the tube was operated at a peak voltage of 200 kv. for the pollen and 250 kv. for the seed exposures.

The plantings were made in sand-benches in the greenhouse at Lincoln, Nebraska, on April 21, 1950, and detailed studies were made for a period of 28 days following planting. Data were taken on germination, stands at various dates, growth rate, exposed leaf number, and other morphological characters.

Chemical analyses of maize pollen and of excised maize embryos were performed by the Chemistry Division of the Argonne National Laboratory, Chicago, Illinois.

Experimental Results

Mean seedling heights on two dates and the mean number of leaves per seedling on one date are presented in Table I. The height trends established on those dates are shown graphically in Figure 6.

Plant height was depressed by radiation of both types at both dates of measurement except in the one-minute pile-irradiated pollen lot. The 1200 roentgen X-radiation of pollen appeared to be more effective in depressing growth than did the 7500 roentgen X-radiation of seed and was approximately as effective in depressing growth as the two-minute exposure of pollen to thermal neutrons. A one-minute neutron treatment of seed was not included, but by interpolation in Figure 6 it appears that such a treatment would have been approximately equal in its effect on seedling height to a 7500 roentgen X-radiation of the seed.

The similarities in average heights of seed-irradiated and pollen-irradiated progenies with the same neutron exposure are striking. However, the low standard errors associated with the seed-treated lots are indicative of the uniform effect in contrast with the wide variation in individual plant effects observed in the pollen-irradiated lots (Table I).

A progressive increase in exposed leaf number appeared to be associated with increase in length of exposure of maize seed to thermal neutrons as shown in Table I. A marked increase was observed for the four-minute and eight-minute exposures as compared with the control and the two-minute exposure.

The effects of the various treatments on maximum stands and stands on the 28th day after planting are presented in Table II. Maximum stands were unaffected by the exposures of seed to various thermal-neutron radiations or to the 7500 roentgen X-radiation. In the thermal neutron irradiated pollen lots, the maximum stand decreased progressively as the exposure time was increased, beginning with the two-minute treatment. Maximum stand dropped to 16.7 percent for the eight-minute pollen irradiation.

Delayed death was observed only following eight minutes of seed irradiation with thermal neutrons. In this lot the stand dropped from a maximum of 98.3 percent to 63.3 percent on the 28th day. No delayed death was observed in the pollen irradiated lots.

One of the most striking seedling effects resulting from thermal neutron irradiation of the seed consisted of narrowness and upright position of the leaves (Figure 5). The seedlings from neutron-irridiated seed were also darker bluish-green in color than those from the control, X-rayed, or pollen-irradiated lots. Other anomalies in seedlings from pile-irradiated seed occurring principally in the third to the fifth leaves and in some cases persisting in leaves above were mottling, light green striping, white striping, slashed leaves, and one-sided leaf development. Many of the abnormalities occurred as mirror images of each other in adjacent tissues. The size and frequency of the chlorophyll-deficient stripes increased with longer periods of pile exposure. The slashed effect was probably due to killed areas in the meristematic tissue.

In the various thermal-neutron irradiated seed lots, the percentage of plants having one

TABLE I. Mean height of F_1 L289 × I205 maize seedlings at 14 and 28 days and mean number of exposed leaves per plant at 28 days following planting of irradiated seed and seed obtained from irradiated pollen.

Treatment	Number days following planting — 14 days — No.* seedlings	Mean height† cm.	— 28 days — No. seedlings	Mean height cm.	Mean exposed leaf no.
None	60	19.7±0.23	60	37.1±0.45	4.9±0.04
X-ray, 7500 *r*, seed	60	18.8±0.18	60	34.7±0.27	4.6±0.06
X-ray, 1200 *r*, pollen	54	17.5±0.58	54	32.2±0.89	4.4±0.11
Nuclear reactor:					
1-min. exposure, pollen	60	20.6±0.21	60	37.4±0.36	4.0±0.02
2-min. exposure, seed	60	15.5±0.19	59	30.1±0.29	5.0±0.04
2-min. exposure, pollen	51	17.2±0.52	51	30.3±0.88	4.5±0.09
4-min. exposure, seed	60	12.9±0.17	60	27.3±0.39	5.4±0.07
4-min. exposure, pollen	35	16.0±0.84	35	27.6±1.33	4.5±0.13
8-min. exposure, seed	59	5.6±0.17	42‡	14.3±0.71	6.3±0.13
8-min. exposure, pollen	10	10.3±1.65	10	20.3±3.26	4.0±0.56

* 60 planted for each treatment.

† Leaves held erect for measurement.

‡ Includes 4 plants only partially green.

or more leaves showing the abnormality was as follows:

Treatments	Light green striping	White striping	Slashed leaves	Wrinkled leaves
2-min. exposure	15	0	8	0
4-min. exposure	40	1 (cream colored)	22	0
8-min. exposure	42	10	31	16

An even more common effect in the eight-minute seed-irradiated lot than those shown above was the one-sided leaf development which resulted in much twisting and curling of the leaves.

The only apparent seedling effects resulting from the 7500 roentgen X-radiation of seed were very slight mottling, slight leaf narrowing, and depression in growth. There were no leaf anomolies nor sectors evident in this lot.

The most readily-observable seedling effect resulting from the pollen irradiations was the height reduction in individual plants. The leaf abnormalities noted for the seedlings grown from the irradiated seed were not observed except for an occasional narrow-leaved, grass-like plant. Yellowish-green seedlings were also observed occasionally. It should be noted, however, that a deficiency of abnormal plants may have resulted because of a failure of kernels to germinate.

Discussion

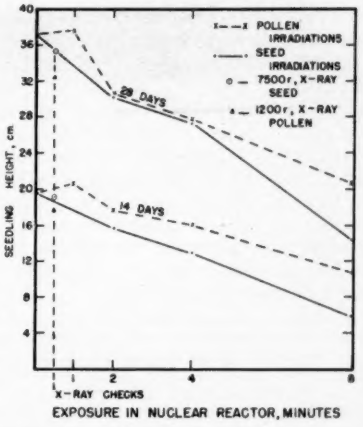
The greater efficiency of thermal-neutron seed irradiation over pollen irradiation in depressing seedling growth, as determined through X-ray comparisons, is the most striking result recorded in these experiments. An examination of the pollen data, Table I, indicates that X-radiation of 1200 roentgens was approximately equal in its effect to two minutes of thermal-neutron irradiation. If this ratio is applied to the seed irradiations, an X-radiation of 7500 roentgens would be expected to be approximately equal in effect to a pile irradiation of 12 minutes. In contrast, in the seed-irradiated series, the 7500 roentgen X-radiation appears, by interpolation, to be approximately equal to one minute of the thermal-neutron irradiation. Thus, on the basis of these X-ray comparisons, it would appear that thermal-neutron irradiation was approximately 12 times as effective on maize seed in depressing subsequent seedling growth as would have been expected from the pollen irradiation effects.

From previous studies involving the same date of pollen irradiation[7], it was found that on August 16, 1948, pile irradiations resulted in effects which were lighter than the average of those on other dates. Using four kernel characters as a measure of comparison, it was found that on August 16, 1948, circa three

TABLE II. Maximum stand and number of plants on the 28th day after planting L289 × I205 hybrid maize seed irradiated or seed obtained from pollen irradiated with various periods of thermal-neutron exposure or with X-radiation.

Treatment	No. kernels planted	Stand: Maximum No.	Stand: Maximum %	Stand: 28 days after planting* No.	Stand: 28 days after planting* %
	Seed				
None	60	60	100.0	60	100.0
X-ray, 7500 r units	60	60	100.0	60	100.0
Nuclear reactor, 2-min. exposure	60	60	100.0	59	98.3
Nuclear reactor, 4-min. exposure	60	60	100.0	60	100.0
Nuclear reactor, 8-min. exposure	60	59	98.3	38	63.3
	Pollen				
X-ray, 1200 r units	60	54	90.0	54	90.0
Nuclear reactor, 1-min. exposure	60	60	100.0	60	100.0
Nuclear reactor, 2-min. exposure	60	51	85.0	51	85.0
Nuclear reactor, 4-min. exposure	60	35	58.3	35	58.3
Nuclear reactor, 8-min. exposure	60	10	16.7	10	16.7

* Plants dead or definitely dying not included.



GROWTH INHIBITING AND EFFECTS

Figure 6

Effects of exposing single-cross hybrid maize seed and inbred maize pollen to thermal-neutron irradiation and to X-radiation on subsequent height of seedlings grown from the irradiated L289 × I205 seed and seed obtained from the pollination of untreated L289 plants with irradiated I205 pollen. (Based on Table I).

minutes of pile irradiation of the pollen were necessary to equal the effect produced by 1200 roentgens of X-radiation of pollen, and that on August 19, 1948, circa one to one and one-half minutes were equal to the 1200 roentgen X-ray check. Thus, assuming that the pollen irradiation series used represents one-half of the average effect expected from a given period of exposure, the effectiveness of the pile irradiation of the seed would still be six times that expected on the basis of the pollen data.

In order to account for the results obtained in this experiment, the type of radiations present in the pile where the materials were exposed must be considered. Since no shielding was employed in either series, the ionizations produced in the tissues were due to gamma ray contamination arising from the pile reactions and to thermal neutron capture. It is assumed that all neutrons were effectively slowed down so that no fast neutron contamination existed.

The amount of ionization due to gamma ray contamination has not been determined. If, however, the radiation effect were ascribed to gamma rays, it would be expected that the effectiveness ratio would parallel that of the X-ray effect. The differential effectiveness noted, however, indicates that the greater portion of the effects produced in the tissues must have been due to neutron capture reactions. Neutron capture is, of course, influenced by the chemical composition of the tissue irradiated. The number of ionizations produced further depends on the capture radiation emitted, the energy of the emission, and the amount of that energy absorbed by the tissue in question. Calculations based on the chemical and spectrochemical analyses indicated that three elements—hydrogen and nitrogen because of their concentration, and boron because of its high capture cross section, accounted for almost all of the immediate ionizations produced by neutron capture. The concentrations and the capture and emission properties which determine the roentgen-equivalent-physical (*rep*) per minute of ionization absorbed in the tissues due to each element are given in Table III.

Analysis of the data of Table III indicates that of the three elements, nitrogen is the most important in the total *rep* per minute of ionization in the tissue due to neutron capture. Because of their short paths, all of the energy of the alpha and proton particles of the boron and nitrogen reactions, respectively, is absorbed in the tissue, while only a very small amount of the energy of the hydrogen-emitted gamma rays is absorbed. The amount of the gamma ray energy absorbed can be estimated as shown by Conger and Giles.[5] The gamma ray effect may have been underestimated since the various seed or pollen samples were in close proximity to each other in the reactor and thereby each sample probably received some gamma radiation from the other samples. The chemical analysis of the pollen may not be truly representative of that irradiated since it was based on a pollen composite obtained from maize grown in the greenhouse at Lincoln, Nebraska, in 1950. However, the soil was not known to be boron deficient. The nitrogen analysis is in reasonably close agreement with that generally reported.

The conversion of the emission radiation energy in *Mev* to roentgen-equivalent-physical (Table III) reveals that with equivalent neutron flux ~95 *rep/min.* of ionization would be expected to be absorbed in the pollen tissue and ~220 *rep/min.* in the embryo tissue. This means that approximately twice the ionization would have been expected in the seed as in the pollen for the same exposure length on the basis of the chemical composition and assuming that the pollen analysis is representative. This is not of the same order as the effectiveness ratio of six to 12 that was observed. It may be that the biological effect or damage with increasing *rep/min.* of ionization due to neutron capture is not a linear but rather an exponential relationship. At any rate, it appears that the greater effectiveness of the pile irradiation on maize seed as compared with its effect on maize pollen, on the basis of X-ray comparisons, must be ascribed to neutron capture reactions and those largely to boron and nitrogen, with the latter being most important. However, because of the greater density of ion pairs per micron path produced by the boron-emitted alpha particle, the importance of the

TABLE III. Components of total *rep* per minute of ionization absorbed in maize pollen and maize embryo tissue partitioned among the capture reactions of hydrogen, boron, and nitrogen. Thermal neutron flux 7×10^{10} neutrons per square centimeter per second. Calculations based on the method of Conger and Giles.[6]

Element	Percent of wet weight*	Capture cross-section	Capture radiation emitted and energy: Type	Energy (Mev)	Fraction of energy absorbed in tissue	*Rep/min.* absorbed in tissue	Percent of total *rep/min.*
			Maize pollen†				
H	8.5	0.32	γ	2.23	0.0021	6.13	6.49
B	0.000,081,5	715.0	α	2.40	1.0	6.21	6.58
N	2.333	1.7	p	0.6	1.0	82.07	86.93
					Total	94.41	
			Maize embryo				
H	8.0	0.32	γ	2.23	0.0016	4.39	2.00
B	0.000,519	715.0	α	2.40	1.0	39.90	18.16
N	4.975	1.7	p	0.6	1.0	175.46	79.84
					Total	219.75	

* B and N analyses by Chemistry Division, Argonne National Laboratory, Chicago, Illinois. H calculated from data presented by Anderson and Kulp[2] for maize pollen and by Winton and Winton[14] for maize embryos.

† Pollen analysis based on a composite obtained from greenhouse plants, Lincoln, Nebraska.

effects due to boron may be far out of proportion to its concentration or even to the related ionization. Thus, while X-ray damage is largely independent of the chemical composition of the tissue irradiated, the damage due to thermal-neutron exposure is considered to be related to the concentration of certain elements of the chemical composition. The amount of damage can be modified by changing the chemical composition of the tissue irradiated. Locher[11] suggested that this tool be used in radiotherapy. Krueger[9] attempted to use boron in this manner, and Zahl *et al.* [15, 16] used boron and lithium, another element with a high capture cross section. While they encountered certain biological difficulties, Conger[4] proved the importance of boron in this connection by showing that boron-enriched *Tradescantia* buds were four to five times as sensitive to thermal-neutron irradiation as unenriched buds.

There is as yet little experimental evidence as to the true ionization and other effects due to the recoil of the emitting nucleus atom following thermal-neutron capture and to the transmutation involved. Hershey *et al.*[8] found that on the basis of equal ionization assimilated P^{32} was 34 times more effective than an external beta source in killing bacteriophage particles. They concluded that the killing effect is a direct result of the nuclear disintegration and is rarely due to the ionization produced by the emitted beta particles. These results suggest the possibility that ionization may not account for all the effects produced by radiations in higher plants and that the effects of X-rays and thermal neutrons may differ qualitatively as well as quantitatively. Since nitrogen is a vital component of nucleic acids, its transmutation to carbon as a result of neutron capture might interfere with the normal functioning of the molecule of which it forms a part. The transmutation of boron to lithium could also conceivably be of importance. This possible importance of the transmutation process has also been suggested by Conger and Giles.[5]

Summary

The susceptibility of maize pollen and maize seed to thermal neutrons was determined through the effects on the subsequent seedling development. X-radiation was included as a basis of comparison.

Both pollen and seed irradiations were made by exposure for periods of 0, one (pollen only), two, four, and eight minutes to a flux of 7×10^{10} neutrons/cm^2/sec. In general, increasing the length of seed exposure to neutrons had the following effects on the seedlings: (1) reduced plant height; (2) increased number of exposed leaves; (3) delayed death (eight minutes only); (4) narrowness and upright position of leaves; and (5) anomalies consisting of mottling, chimeras, slashed leaves, one-sided leaf development, a darker bluish-green color, light green and white stripling, and wrinkling of leaves. Increasing the length of pollen exposure to neutrons had the following effects: (1) reduced plant height and (2) decreased maximum stand. A striking similarity was noted in average heights of seedlings from irradiated seed and seed from pollen irradiated with neutrons for the same periods of time. The standard errors for the latter, however, were much higher than for the former.

On the basis of X-ray comparisons, thermal neutrons were circa six to 12 times as effective on maize seed as on maize pollen in reducing subsequent seedling height. Even if allowance is made for the greater amount of ionization produced in seed than in pollen by equal doses of thermal neutrons, there is still a large difference in the efficiency of these particles on the two plant parts (on the basis of X-ray comparisons). It is, therefore, suggested that ionization alone may not account for all of the biological effects of thermal neutrons and that transmutation of nitrogen to carbon and/or boron to lithium may also contribute to the biological effects.

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A NOTE ON TONGUE ACROBATICS

High Incidence of "Clover-Leafers" Found in Virginia College

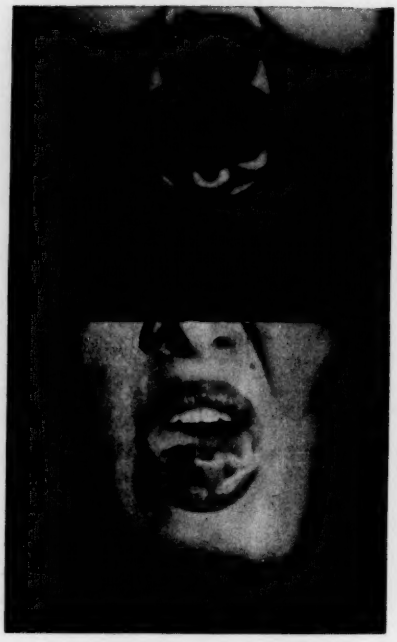
A NOTE by Milton O. Hoch in the May, 1949 issue and by David D. Whitney in the July, 1950 issue of THE JOURNAL OF HEREDITY indicated that the ability to form a "clover-leaf" with the tongue may be a rare talent. A survey of a group of 163 girls at Mary Baldwin College made by the members of a class in a course in genetics revealed 11 who possess this ability. Figure 7 shows the performances of two.

Four types of tongue movements were investigated: (1) rolling the tongue into a tube; (2) twisting it corkscrew-wise so that the lateral edges are dorsal and ventral; (3) overfolding the tongue tip in any fashion; and (4) the "clover-leaf." The interviews to determine the individual abilities of the subjects investigated were carried out in the dormitory rooms occupied by the students.

Forty-one girls were unable to exhibit any of the four types of movement described above. Some of the subjects may not have made a very earnest attempt to perform these feats. Fifty-one girls were found who could roll the tongue into a tube. Twenty-six could roll the tongue and also twist the tongue. Persons with all combinations of abilities to execute the first three movements were found, including four whose only aptitude was overfolding the tip.

Five of the eleven "clover-leafers" could perform all four movements. Four could do all except form the tube, one could form the tube but could not fold or twist; and one girl was a "clover-leafer" only.

No attempt was made to obtain information concerning the abilities of other members of the family of these girls except in the case of the eleven "clover-leaf" group. Six girls reported that no member of the immediate family could execute the "clover-leaf." Fathers could in two instances; the mother and a grandmother in one; a brother in one, and a sister in one. These findings seem to indicate that the ability to form a "clover-leaf" with the tongue is not an excessively rare gift, and suggest that it may be rather simply inherited.



TONGUE VIRTUOSOS

Figure 7

Here shown are two superb examples of the 'clover-leaf" trick. This frequency of about seven percent is higher than has previously been reported.

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PINTAIL, A DOMINANT MUTATION

Linked with Brown in the House Mouse

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PINTAIL PHENOTYPES

Figure 8

Variation in tail length and form of pintail heterozygotes, as contrasted with four normal tails. Homozygous pintail individuals are similar to the group here having the shortest tails.

EVIDENCE has previously been reported which indicates that the powerful carcinogenic substance, methylcholanthrene, may also be mutagenic in mice.[4,5] The present paper deals with one of the more interesting mutants obtained in a strain protractedly treated with this carcinogen.

The original mutant, ♂74,488, appeared in the 21st generation of sib inbreeding of the "pBr" strain, which has the genetic markers *a a* (non-agouti),

*This experiment has been made possible by grants from the Jane Coffin Childs Memorial Fund for Medical Research and The Anna Fuller Fund.

b b (brown) and *p p* (pink-eye). The tail of this mouse was about two-thirds normal length, and the distal end showed a peculiar thin and somewhat distorted tip. The name "pintail" has been chosen for the trait.

Somewhat similar tail anomalies had been found occasionally in this and other strains of the laboratory, but none had proved heritable before. The present mutation, however, is clearly inherited as a dominant. It has been outcrossed to mice of various other strains for genetic study, including linkage tests.

The pintail descendants have been markedly variable in tail length and shape, but seldom would be confused with normals. There is evidence that some of the variation is genetic; pintail F_1 mice from crosses with the C_{57} black strain have generally been classified as "slight," approaching normal, while those from crosses with the short-eared JK-strain have usually had tails about half normal length. These are extreme examples for F_1; but backcrossing to the short-eared stock produced some young with extraordinarily short and thin tails. These mice are all clearly heterozygous for the pintail gene, and may be short-eared or not—the short-ear gene is obviously not responsible for the variation. An assortment of the length variations in heterozygotes is shown in Figure 8.

X-ray photographs and alizarine-red staining have revealed that the proximal vertebrae of the tail are indistinguishable from normal, while distally a change is seen, often abrupt, usually involving reduction of size, some distortion, slipping out of line, and finally complete elimination of vertebrae. The most nearly normal pintail individuals have had at least five less caudal vertebrae than normal, while the extremely short pintails lack 20 or more. In the latter cases the visible external part of the tail may be half an inch long and contain no vertebrae (Figure 9).

The pintail trait is almost as easy to recognize in newborn young as in adults. The tail of the normal newborn mouse has a smooth contour and a blunt tip; that of pintail is more irregular in contour, usually with one or more constrictions, and has a characteristic filiform tip. In the more pronounced cases even half or more of the tail may be thin, and may be bent down and reflexed somewhat like a safety pin. Classification in late fetal stages is also possible, but a dissecting microscope is needed for certainty. Just when the trait is first recognizable in the embryo has not been ascertained. It will be interesting to discover whether the reduction of vertebrae of pintail mice is due to failure of formation or to degeneration.

Linkage Relations

In linkage tests the pintail trait has shown about 5 percent crossing over with brown, but independence with relation to other markers (Table I). All of the linkage tests were of the backcross type. It is desirable to analyze the results with brown in regard to sex and phase of the heterozygotes (Table II). Mortality in the young before classification was negligible (8.5 percent) and is omitted from

TABLE I. Linkage tests of Pintail with six other genes.

Linkage Test with	Offspring total	Offspring cross-overs	% crossing over	Stand. errors
a *	303	164	54.1 %	±2.9%
b	629	32	5.09%	±.87%
c **	38	18	47.4 %	
p *	32	16	50.0 %	
s **	144	75	52.1 %	±4.2%
ss	26	13	50.0 %	

* repulsion phase only
** coupling phase only

TABLE II. Linkage tests of Pintail and Brown.

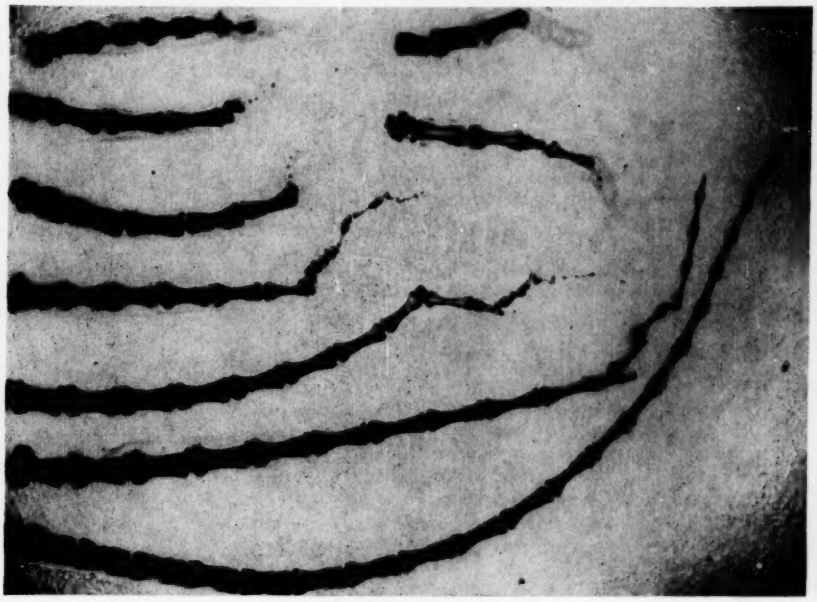
Heterozygote Sex	Phase	Offspring Total	Offspring Cross-overs	% Cross-overs	Standard errors
♂	coupling	116	4	3.45%	
"	repulsion	272	15	5.52%	
"	total	338	19	4.9 %	± 1.1%
♀	coupling	10	1	10. %	
"	repulsion	231	12	5.2 %	
"	total	241	13	5.39%	± 1.5%
♂+ ♀	coupling	126	5	3.97%	
♂+ ♀	repulsion	503	27	5.37%	
Total		629	32	5.09%	± .87

TABLE III. Segregation Ratios of Pintail and Normal in F_2.

Data	Number litters	Total offspring	Dead fetuses	Offspring classifiable short	medium	slight	normal	% normal
Prenatal	49	451	28	80	46	179	118	27.9%
Postnatal	124?	793*		168	159	262	200	25.3%
Total					893		318	26.24%
								± 1.26%

* 4 not classifiable (tails chewed)

NOTE: Too late to correct, two errors were discovered in these tables. In Table II, 338 should read 388, and in Table III 893 should read 894.—Ed.



VERTEBRAL STRUCTURE

Figure 9

The tail of a normal mouse (below) compared with the tails of eight pintail mice, cleared and stained with alizarin red to show the vertebral arrangement. Note outline of distorted tail tip lacking vertebrae in extremely short specimens.

consideration. It appears that there is no significant difference in crossing over between coupling and repulsion phase nor between males and females. The latter finding is in contrast with the considerably greater crossover percentage from females in linkage tests between the markers *c* and *p* as reviewed by Grüneberg.[1]

A study of the F_2 ratio (produced from pintail heterozygotes) shows close approximation to the theoretical 3 : 1 segregation, both before and after birth (Table III). Only fairly late fetal stages were included in prenatal counts. It is clear that the number of dead fetuses is within usual range, and litter sizes are normal,[2] so that the homozygote does not die in utero. There is a marked discrepancy between the two groups (prenatal and postnatal) with regard to average litter size; this difference appears to be an incidental result since the females of the two groups were of considerably different origins—the former involving more heterosis.

The close linkage of pintail and brown permitted identification of the homozygotes from matings of two repulsion-phase heterozygotes, most of the brown offspring being of the homozygous pintail type. The homozygotes have been short-tailed or occasionally medium-short. They are on the average smaller than their litter mates, and there is a high mortality rate, apparently due to digestive troubles, before weaning age. Several homozygotes so far have shown anatomical abnormality of the perineal region; two were males with imperforate anus, the intestine opening into the urethral region. Imperforate anus with fatal results has also been observed in a few individuals within a few days after birth.

In spite of the unpropitious beginnings of most homozygotes, a fair number can survive and when mature maintain normal health. They generally breed well in crosses. Perpetuation of the stock is hazardous from matings of homozygotes together, but not impossible; at present seven pairs have successfully raised some offspring.

The linkage relations of pintail and brown, and the viability of the pintail homozygote are clear evidence that it is not an allele of previ-

ously known tail mutants[8] such as brachyury (*T*). Therefore we propose that pintail be assigned the symbol *Pt*.

Summary

A new dominant mutation, "pintail," appeared in an inbred, methylcholanthrene-treated strain of mice. The principal feature is a reduction in number of caudal vertebrae. Genetic modifiers are shown to be important. The trait shows close linkage (5 percent crossing over) with brown. Homozygotes are viable until birth, and some mature and breed normally; often however growth before weaning is inferior and there is high mortality. A few have had imperforate anus. The symbol *Pt* is proposed.

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The Genetics of The Mink

ARTHUR W. King, who is the author of several articles in the "American Fur Breeder," including a "Practical Mink Breeding Guide," has attempted to organize current knowledge on the genetics of mink in such a form that it can be readily used by practical fur breeders, and with the hope they may be encouraged to make systematic efforts toward further progress.

The book* is written with a clarity which might well be a model for textbook writers who have attempted to interpret genetics for the student. It is introduced by an excellent glossary on genetic terms and then proceeds to chapters on various special problems.

In the first chapter evidence is presented that enough different characteristics have accumulated in certain varieties of mink so that they may begin to be called breeds. The mutant types are described, and the author attempts to reduce genetic symbols to a standard system which will be convenient for mink breeders. A question of policy may be raised as to whether this should properly be done by one author, or whether it should be done by general agreement among the workers concerned as has been the case when similar problems arose in other animal species. 22 reported mutations for fur color are listed, in 17 different loci. Ten other possible mutations, mostly of body abnormalities, are also listed.

Practical chapters on diseases and freaks, the use of pedigrees, and economic pelt production follow. The book concludes with brief comments on heredity and environment and detailed descriptions of the appearance of various commercial fur colors.

There is an extensive bibliography covering both trade and genetics journals, but this is often not referred to in the text. There is an index, and the book appears to be well organized for practical use. It should be very useful to fur breeders, and theoretical geneticists should find it helpful as an introduction to the genetics of a species in which a surprising amount of progress appears to have been made.

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*A. W. KING, *Genetics of Mink;* a handbook for the student and rancher. 183 pp., 7 plates, 4 figs., 2 charts. International Publishing Co., Duluth, Minn., 1951.

SPONTANEOUS AND INDUCED VARIATIONS IN MITOSIS

G. B. Wilson, Mary E. Hawthorne, and Te May Tsou*

In a series of papers[3, 4, 5, 6] dating from late 1947, C. L. Huskins has discussed the occurrence and potential importance of a variation in the course of mitosis which since has been generally referred to as "reductional groupings." Essentially such "groupings" involve the separation of whole chromosomes into two or more groups. If this initial separation is followed by separation of the chromatids, as appears to be the case in some instances, both genetic segregation and reduction may take place. Since, to a degree at least, the end result is similar to that of meiosis, the implication was that a form of nuclear division, equivalent to that preceding gametogensis or the formation of the gametophytic generation, was occurring. The phenomenon was, therefore, frequently referred to as "somatic meiosis." The major objection to this terminology, as Professor Huskins has pointed out[4], is that the generally held concept of meiosis does not encompass the mechanics of these "somatic reductions."

Huskins' original observations were made on materials treated with solutions of sodium nucleate. Since nucleic acid is an essential cell constituent, the idea that there was a specific relationship between the chemical used and the results obtained was virtually inevitable. Even the fact that cold[5] and inorganic phosphates[2] led to the same result and also the fact that "reductional groupings" were noted in untreated material did not constitute proof of lack of specificity, since all of these, in one way or another, could be more or less directly related to nucleic acid "metabolism." The subsequent discovery that a large number of apparently unrelated chemicals appear to be equally effective in inducing "reductional groupings"[1, 11] suggests that we are dealing with a generally, rather than specifically, determined reaction. However, Allen, Wilson and Powell[1] noted certain points of difference between the effects of colchicine and sodium nucleate and suggested that the similarity between the two chemicals may be superficial. Later studies on the effects of colchicine, particularly those of short treatments, have indicated that some of the originally noted differences are variations of degree rather than kind. None the less, Levan and Lofty's[9] implication that the effects of colchicine and sodium nucleate are essentially the same is not entirely acceptable. We still have reason to believe that they are not. However, the major differences appear to be concerned with necrosis and to have little to do with the induction of "reductional groupings."

Sources

The illustrations in the present paper are taken from onion root tips treated with cyclochlorohexane, Acti-dione, or simply grown in tap water. The figures indicate our current opinion concerning the ontogeny of "somatic reductional mitosis" and its place amongst the more or less orderly variations in mitotic activity. The treatments used have no particular bearing on our present thesis.

The gamma isomer of cyclochlorohexane is

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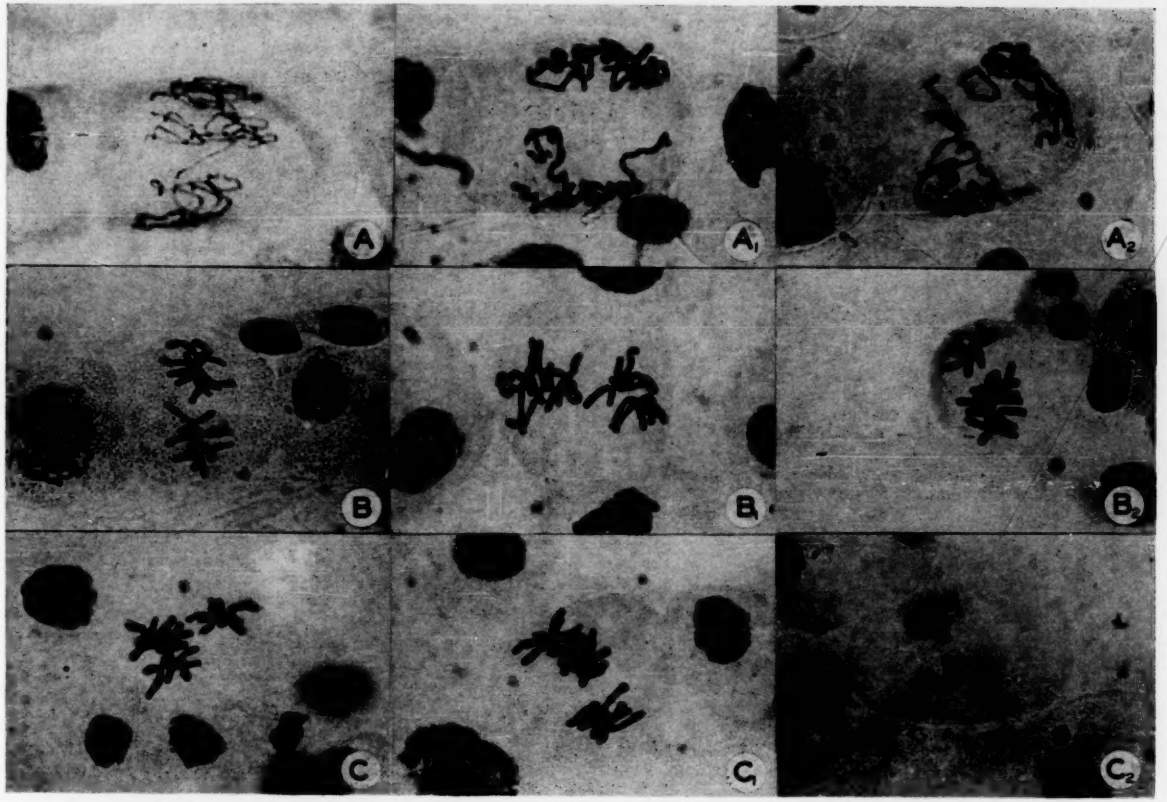
We wish to express our indebtedness to: The All-College Research Committee and the Michigan State Agriculture Experiment Station for financial assistance; the Upjohn Company, Kalamazoo, Michigan for supplying us with Acti-dione and other antibiotics; the Dow Chemical Company, Midland, Michigan for supplying us with Lindane as well as with pure samples of all five known isomers of cyclochlorohexane; and Mr. Philip G. Coleman for photography and preparation of the plates.

Contribution No. 51-7 from Department of Botany and Plant Pathology, Michigan State College, East Lansing, Michigan.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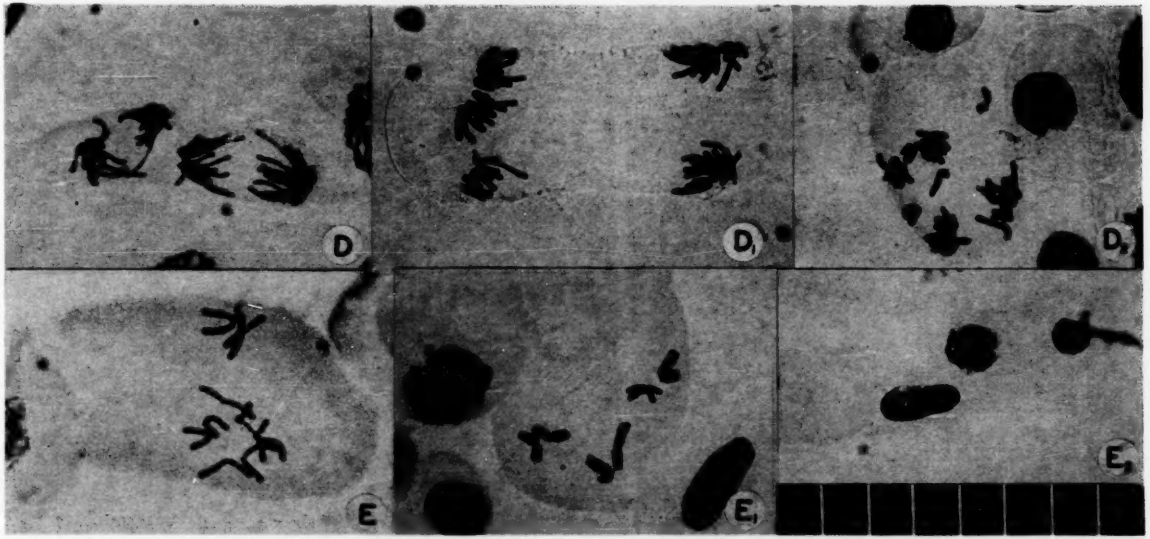


REDUCTIONAL TYPE MITOSES WITH AND WITHOUT TREATMENT

Figure 10

Three series of "Reductional Type Mitoses" in onion root tips are shown above. The left-hand series (*A-E*) are from preparations treated with "Lindane." The A_1-E_1 series are from untreated root tips. The A_2E_2 series are from Acti-dione-treated root tips. Each division on the scale (lower right) represents ten microns.

the active ingredient of a number of commercial insecticides. For the most part we have used a Dow Chemical Company preparation called "Lindane" which consists of 25 percent wettable, active ingredient mixed with an inert carrier. Kostoff[7, 8] has shown that similar insecticides have an action which, in general, resembles that of colchicine especially in being potent polyploidizing agents. These results have been confirmed and will be discussed in a subsequent paper.

Acti-dione is an antifungal antibiotic produced by *Streptomyces griseus*. Its general cytological effects have been discussed briefly in an earlier paper.[11]

Procedures

During the course of our program of testing the cytological effects of a number of organic compounds, we have established the more or less standard technique of rooting onions in tapwater and transferring the rooted bulbs to solutions or suspensions of the test material in distilled water. Periodically controls were run in distilled water during the period of the experiment. For the most part, preparations have been made by the Feulgen squash technique but enough sections have been cut to confirm general observations.

Observations and Discussion

Figure 10 illustrates stages in the process of somatic reduction after treatment with 0.1 percent "Lindane" and subsequent recovery for several days (*A*—*E*); for untreated material (A_1—E_1), and after Acti-dione treatment (A_2—E_2). So far we have been unable to find actual reduced cells in division after the Acti-dione treatment, presumably because, after the majority of our treatments, division ceases before a given cell can go through a second cycle of mitosis. A logical sequence of stages may be arranged, i.e., split prophase giving rise to split metaphase and the latter giving way to split anaphase. A cell, therefore, may develop from two to four or more nuclei depending on the number of original groups, the orientation and the degree of separation of polar groups. Cytokinesis would then give rise to some cells with a reduced number of chromosomes which may or may not be capable of further division.

There is, of course, no certainty that the sequence is a regular occurrence or, indeed, that it exists at all. It is quite possible that the separation may occur at any stage. Until we are able to watch the process in action, there appears to be no way of making certain that one stage gives rise to the next in line. In the cases illustrated in Figure 10, aside from the cleavage, the spindle apparatus appears to be essentially normal. Examination of split metaphases in sections have shown that, in some cases at least, each group has its own spindle. The majority of split metaphases appear to be aligned in the same plane which increases the chances of reversion to the normal situation at telophase. In cases where the two elements are not in the same plane (as in Figure 10*C*) anaphase figures such as shown in Figure 10*D* are to be expected.

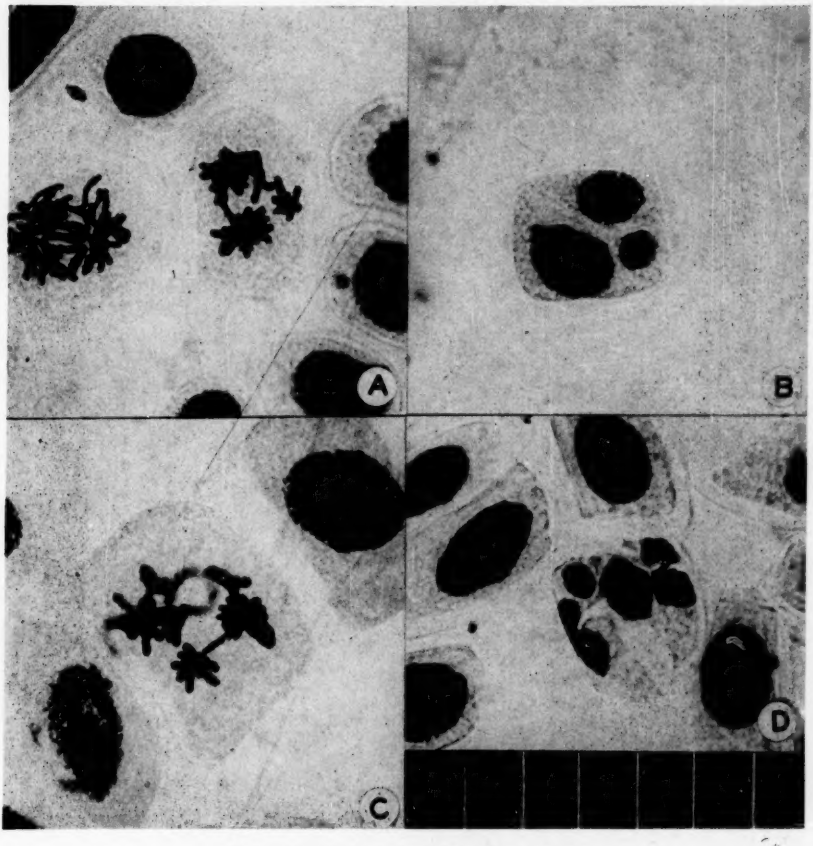
Figure 11 illustrates what appears to be a slightly different type of anaphase breakdown than that shown in Figures 10*D*, D_1 and D_2. After short treatments (approximately three hours) with "Lindane" the majority of anaphases are multipolar. It is not certain that these anaphases are preceded by a complex variant of metaphase more or less equivalent to that shown in Figure 10. Such evidence as we have at present indicates that they are not, but rather that the breakdown occurs during the process of anaphase separation itself. In any case, the end result is a multinucleate cell which, after undergoing cytokinesis (Figures 11*B* and *D*) gives rise to cells with reduced chromosome number (Cf. Levan and Lofty[9]). On the basis of chance alone some of these should be sufficiently balanced chromosomally to survive.

Figure 12 shows four variations in mitosis all of which, at least potentially, are capable of giving different results and all of which may occur in the same material, treated or not. Figures 12*A*—*B* show the normal type of metaphase and anaphase organizations which lead to the production of genetically and cytologically equivalent daughter nuclei. Figures 12*C*—*D* show a split metaphase and anaphase which are potentially capable of leading to both chromosome reduction and genetical segregation. Figures 12*E*—F show split figures without either metaphase organization or typical anaphase orientation. This situation is potentially capable of leading to genetical segregation without reduction in chromosome number. Figures 12*G*—*H* show unsplit figures without either metaphase organization or typical anaphase orientation, a situation which is capable of leading to polyploidy.

The type illustrated in Figures 12*A*—*B* is the dominant form in untreated somatic tissue, while that in Figures 12*G*—*H* is dominant in materials which have been treated with a variety of chemicals. Whether polyploidy actually ensues depends on whether the action of the drug can be stopped at the proper time. This can be easily accomplished with either "Lindane" or colchicine but is extremely difficult with sodium nucleate and Acti-dione. The types of divisions shown in Figures 12*C*—*D* and Figures 12*E*—*F* are relatively rare after all treatments, the first being more frequent in untreated tissues, or after very short treatment, and the second after longer applications.

Conclusions

There does not appear to be any specific relationship between treatment and the occurrence of either "somatic reductional mitosis" (Figures 12*C*—*D*) or



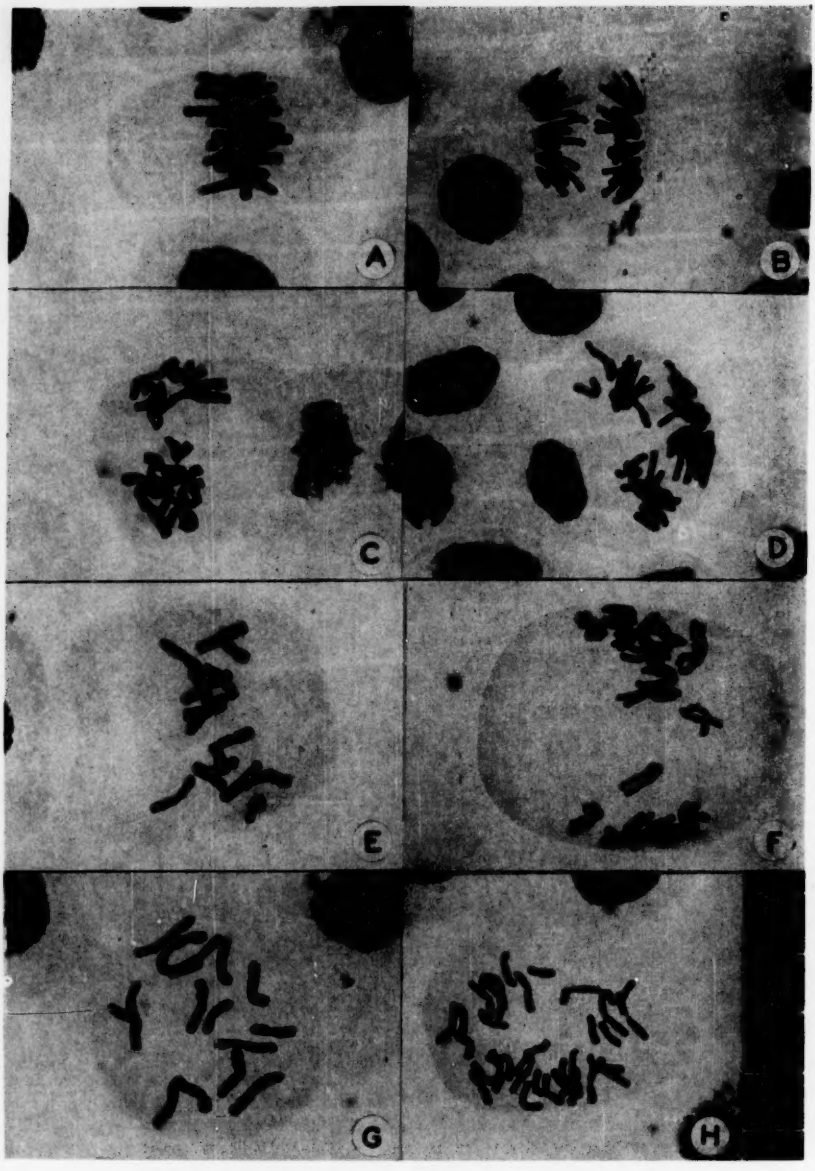
GENESIS OF MULTINUCLEAR CELLS

Figure 11

A and *C*—Multipolar anaphases appearing after treatment with 0.1 percent "Lindane" for three hours. *B* and *D*—Multinucleate cells recovered from such root tips twenty-four hours later. Each division on the scale represents ten microns.

"somatic segregational mitosis" (Figures 12*E*—*F*). Both of these types of divisions occur sporadically in untreated materials and the best that any chemical or physical treatment (of which we are aware) can do is to raise the incidence slightly. In so far as we can see, neither of these types of division is related to meiosis as the term is generally understood. In the first place the initial separation is at right angles to the spindle, where it exists, and any tendency for the pairing of homologues would militate against obtaining a balanced end product. Nonetheless, the potential result may be, in its major aspects, equivalent to that of meiosis without crossing over.

It would seem to us that a careful study of the more or less regularized variations in mitosis such as discussed in this paper should give some clues to the nature of the mitotic mechanism and the



"REDUCTIONAL" AND "SEGREGATIONAL" MITOSES

Figure 12

A and *B*—Normal metaphase and anaphase. *C* and *D*—Metaphase and anaphase of "reductional somatic mitosis." *E* and *F*—"Metaphase" and "anaphase" of "segregational somatic mitosis." *G* and *H*—"Metaphase" and "anaphase" leading to polyploidy. Each division on the scale represents ten microns.

types of forces involved. So far we can offer only a speculative explanation. In the first place, we are unable to see how the spindle can be considered as a single unit which is the basis of most theories of chromosome mechanics (Cf. Shrader[10]). We would like to suggest that there are at least two more or less independent components: 1. a dipolar cytoplasmic orientation possibly characteristic of the cell at any stage; and 2. a nuclear component inherent in and directed by the chromosome or the kinetochore thereof. We would further suggest that metaphase organization is primarily a function of the cytoplasmic component whereas anaphase separation is a function of the chromosome itself. This notion at least avoids the difficulty of explaining, as most theories attempt to do, both metaphase congregation and anaphase separation as a response to the same force. On this basis, split, but otherwise organized, figures (Figures 10*A,B,*and C) would represent a degree of weakness in cytoplasmic orientation. Multipolar anaphases would represent almost complete breakdown of cytoplasmic orientation without serious disruption of the nuclear component. Completely disorganized metaphases and anaphases (Figure 12 *E—F*) would indicate the elimination of both components.

In general, it is our opinion that these various forms of reductional and segregational divisions are intermediate between "normal" and complete lack of spindle organization. Huskins and his associates have discussed the theoretical and practical significance of this type of variation and with their stand we are in substantial agreement. If some means can be found to induce such variations with high frequency without unduly affecting the survival potential of the treated tissue, many genetical analyses, especially those relating to the make-up of complex hybrids, would be accomplished more easily than present techniques permit. In any case, these variations in the mitotic theme appear to offer the most logical explanation of spontaneous reduction[5] and at least some cases of somatic segregation.

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SIMPLIFIED MINK GENETICS

A BOON is offered to mink breeders and an important contribution made to mammalian genetics in this book* by an exceptionally well qualified author. Dr. Shackelford has a boyhood background of first hand acquaintance with the fur industry, was grounded in genetics as a pupil and assistant in research to the late L. J. Cole, and has had a decade of experience in studying the genetics of mink and foxes on ranches and in his own breeding experiments at the University of Wisconsin. As an agent of the Bureau of Animal Industry, U. S. Department of Agriculture, he has had much experience in presenting the results of his studies to mink ranchers having a limited knowledge of the principles of genetics. Out of this has grown an excellent example of good scientific writing for non-technical readers in language which they are capable of understanding.

The breeding in captivity of captured wild foxes and mink was begun in the early years of the century as a means of supplementing a diminishing supply of pelts taken by trappers. The black or silver fox was a rare mutant of the common red fox first observed in a wild state in Prince Edward Island, Canada. It was successfully bred in captivity by Charles Dal-

**Genetics of the Ranch Mink.* Richard M. Shackelford. Pilsbury Publishers. New York City. 1950. 91 pp. 23 figs. $5.00.

ton and Robert Oulton about 1910, and became the foundation of an important industry. Stimulated by this example, mink ranching soon came into being. This involved rearing in captivity and intercrossing wild individuals of several different but fully interfertile subspecies among which those of Ontario, Hudson Bay and Alaska are especially important.

Among the ranch bred mink, color variations (mutations) were observed but commonly discarded until about 1940. The exploitation at that time of the platinum or silver blue, caused a sensation. This valuable novelty, true breeding because recessive in heredity, was capable of rapid increase. Since then, mutations have been carefully looked for and exploited when found.

Shackelford lists thirteen different simple color mutations involving genes at eleven genetic loci. At two loci two different mutant alleles are known. Nine of the mutations are recessive to natural dark and four are dominant.

The author explains Mendelian inheritance with examples familiar to breeders. The first of these, platinum, is recessive in crosses with standard dark, and gives three dark to one platinum in F_2. In this exposition, as in all the other examples, he makes use of excellent figures, easily understood.

Next, dominant inheritance is explained in a cross of royal silver with standard dark, producing royal silver in F_1 and three royal silver to one standard dark in F_2.

Dihybrid inheritance is explained in a cross between two different recessive blue mutations, platinum and imperial platinum, similar in phenotype but distinct in genotype. The crossing of these two mutations results in atavistic standard dark in F_1, heterozygous for both *p* and *ip*; and F_2 gives a typical dihybrid ratio of 9 standard dark : 3 platinum : 3 imperial platinum : 1 sapphire (the combination double recessive).

Most mutations of mink are supposed to be located in different chromosome pairs, of which there are 14 in mink.

One case of linkage is described in which the genes for pastel (*b*) and ebony (*E*), one recessive the other dominant, are shown to be borne in the same chromosome pair with a crossover frequency of 26 percent.

A useful exposition is made of the theory of probability, illustrated in coin tossing, as applicable to the expected frequency in litters of varying size of dominant or recessive phenotypes respectively.

Several mutations in characters other than color are described. These include variations analagous with those known in rodents, such as naked, curly hair, rosette (comparable with the rough coat of guinea-pigs), hydrocephalus midget, (body short but head and feet of normal size), bobbed (a dominant short tail or tailless mutation).

This little book is a model of good scientific exposition, genetically sound, and well illustrated.

W. E. Castle

University of California, Berkeley.

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BETTER LATE THAN NEVER

At the Jubilee Meeting of the Genetics Society of America held at Columbus, Ohio in September, 1950, there was no little sound, some fury, and no unanimity concerning the privileges and duties of scientists to speak out regarding the dangers of political orthodoxy in science. The issue centered around the events in the Soviet Union, which culminated with the genetic purge of 1948. (See the Journal of Heredity for July 1949).

At the Columbus meeting three hours of discussion revealed that many geneticists had not made up their minds regarding this issue. At one point in the proceedings, a committee on Public Education and Scientific Freedom cast into semi-limbo at the New York meeting the year before, was voted out of existence. This action was re-considered, and the committee was finally recreated. The meeting took no stand, however, on the thorny question of whether science by political fiat was a good idea or not.

It is encouraging to report that in Minneapolis on September 11, 1951, a resolution brought in by this Committee, condemning political control of scientific thought, was unanimously adopted by those present at the meeting. The text of this resolution is as follows:

RESOLUTION

"Whereas an official doctrine of genetical theory has been adopted in the U.S.S.R., and the proponents of contrary views have been denied the elementary privilege of intellectual freedom, and,

Whereas similar policies are being adopted in other Communist countries

Be it resolved that the Genetics Society of America condemns these practices, and protests against the establishment of an official orthodox body of theory in any scientific field."

RESEARCH ON GENETICS AND SOCIAL BEHAVIOR

At the Roscoe B. Jackson Memorial Laboratory, 1946 - 1951—A Progress Report

J. P. Scott and John L. Fuller

CONSIDERABLE interest was aroused by the announcement in this Journal in 1945 that the Rockefeller Foundation had given the Roscoe B. Jackson Memorial Laboratory a large grant for the purpose of studying heredity and social behavior in mammals and particularly dogs, thus laying a foundation for extensive studies on many vexing problems of psychology and mental health. During the first year, work was largely concerned with setting up laboratory and animal quarters, and with the organization of a research conference held in the fall of 1946[15]. At that time it was estimated that the project would require at least ten and possibly fifteen years for completion. Since the final results will not be available until that time, it seems appropriate, at the end of the first five years of work, to make a progress report and to summarize the important findings obtained to date. In addition, workers at the laboratory have completed many briefer projects peripheral to the purpose of the grant, but these are available in print and will not be summarized here.*

The General Plan

Since most of our practical problems of behavior are social in nature and since almost every type of behavior shows some degree of sociality it was decided that the social behavior of the dog and its heredity should be studied from the broadest possible point of view. This implied that every individual would need to be thoroughly studied in a large variety of situations and, as the plan has worked out, about fifty individuals are raised per year and over a hundred measures obtained on each animal in twenty-eight different situations. This behavior is studied in an environment which is as nearly optimum for the species as can be obtained, and in which environmental variables are kept as constant as possible.

The research plan included the following steps:

1) A survey of basic behavior patterns in the dog and their variability;
2) A study of the development of the principal patterns of social behavior from birth until 16 weeks of age and older;
3) The development of a variety of tests and measures of behavioral and physiological characters in order that comparisons could be made between selected dog breeds;
4) An experiment on cross-fostering between pure breeds which would test the effects of maternal environment on behavior;
5) A crossbreeding program between breeds which appear to be outstandingly different.

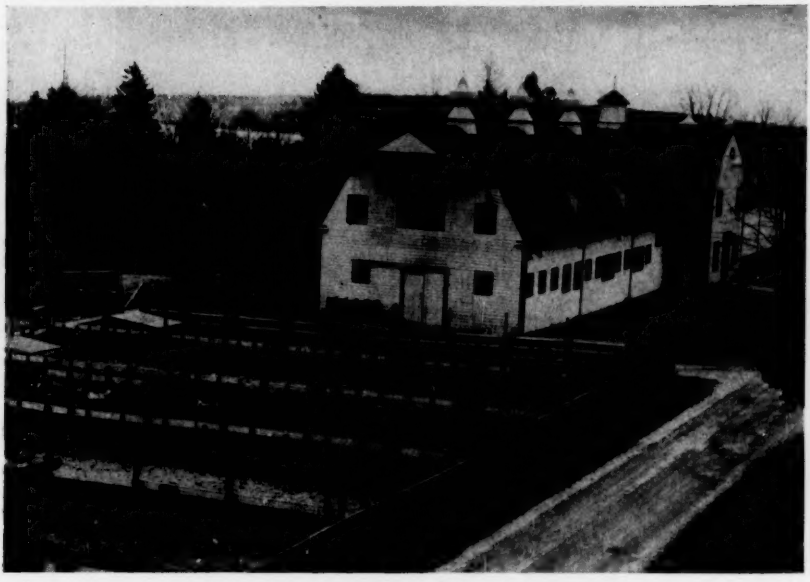
At the present time the first three parts of the program have been largely completed, and the results are outlined below.

*It is impossible to thank individually all of the workers who have contributed their help to this program, but the authors would particularly like to express their appreciation to Dr. C. C. Little, without whose wise administration and experienced advice the program would have been impossible, to Dr. Emil Fredericson for his advice and help on psychological matters, and to the many cooperating summer investigators who have contributed their research, including C. S. Hall, Benson Ginsburg, Elizabeth Beeman, W. T. James, Sherman Ross, Joseph Royce and others.

TEST-BREEDS AND PUPPY NURSERY

Figure 13

A—The five breeds which are currently being studied intensively at the Jackson Laboratory. Left to right: Wire-haired Fox Terrier, Cocker Spaniel, Basenji (African barkless), Shetland Sheep Dog, Beagle. Crosses between Cockers and Basenjis are now under way. Dr. J. P. Scott is holding the dogs. *B*—Interior of one of the nursery rooms for young puppies. In these spacious and well-lighted rooms the puppies spend the first four months of their lives. Dr. Scott is making observations on a young Shetland Sheep Dog puppy.



HAMILTON STATION BEHAVIOR LABORATORY

Figure 14

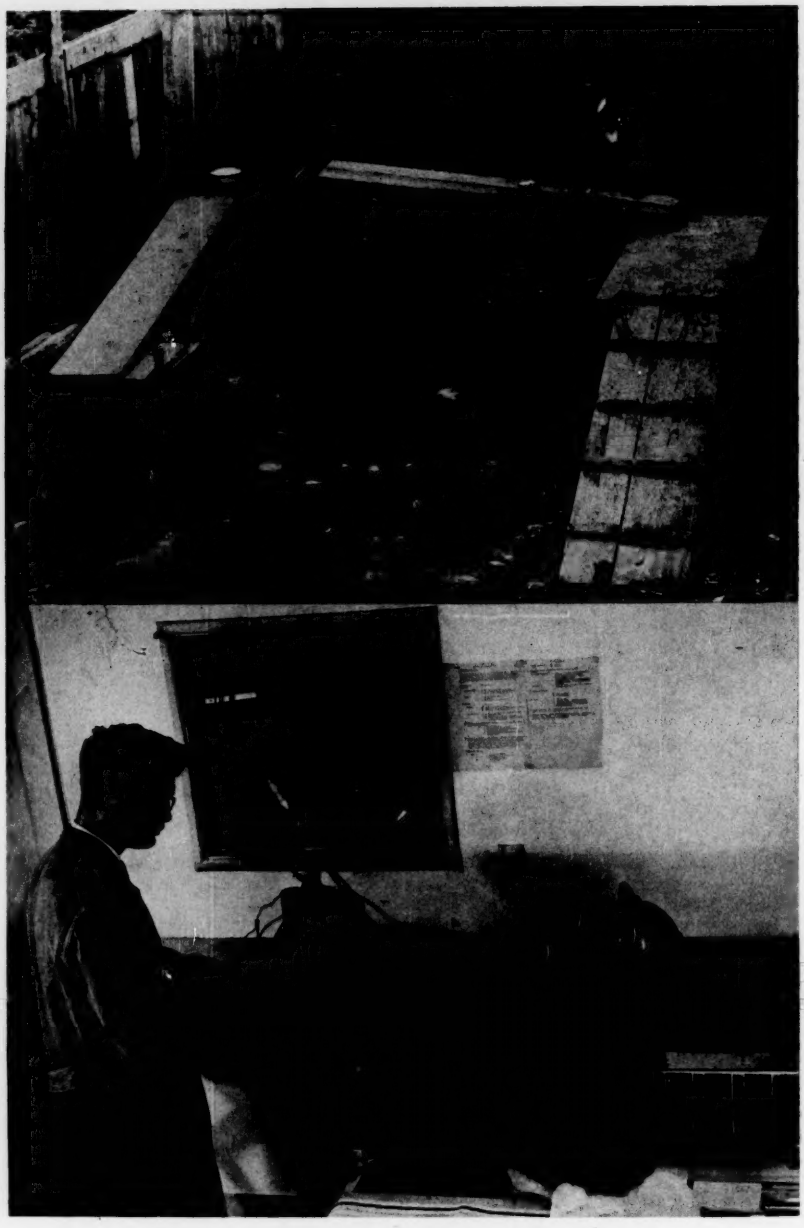
The pens in the foreground are occupied by older puppies (four to 12 months). The nearer wing contains the puppy nursery. The testing laboratories are located in the far end of the building.

Basic Behavior Patterns in the Dog

The survey of basic behavior patterns was done by raising litters of several pure breeds in large one-acre fields and observing their behavior while they were not responding to people.[16] It appeared that dogs respond toward other dogs in the same way that they respond to people and that when dogs and people interact the result is a merging of human and animal social organizations. This concept may be applied generally to problems of taming and domesticating wild animals, as it would appear that those species which are easily domesticated are those which show a high degree of sociality in the wild.

Comparison of these behavior patterns with those found in the wolf by other observers indicates that centuries of domestication and selection have produced nothing which is essentially new but rather that certain patterns of behavior found in the wolf have been either suppressed or emphasized in various dog breeds. The greatest changes have been produced in agonistic behavior where dogs may be either more aggressive or, usually, more submissive than wolves, in investigative behavior as found in the various sorts of hunting breeds, and in allelomimetic behavior (tendency to do the same thing at the same time with some degree of mutual response) with respect to attraction toward people. Dependence upon human beings has been increased and with it et-epimeletic behavior (calling or signalling for care and attention). Epimeletic behavior (giving care or attention) has been decreased and made more variable in regard to the care of the young, while the annual and seasonal cycles of sexual behavior have been modified in most breeds. Other basic behavior patterns such as digestive, eliminative and contactual behavior have been only slightly modified.

Domestic dogs seldom have the opportunity to develop an independent social organization similar to that found in wolves. The most important natural social relationship found in dogs is that between litter mates, which tends to result in pack formation in the adults. The parent-offspring relationship is somewhat less important. The relationship developed between dogs and human beings is similar in many ways to the human parent-offspring relationship and hence can be used for experimental work on many aspects of child psychology. Dominance relationships are very important



TESTS FOR ORIENTATION AND REACTIVITY

Figure 15

A—African Basenji on spatial orientation test. The animal is graded on its ability to immediately recognize the correct path to the goal. The path is changed at each trial. *B*—The reactivity test. Physiological and emotional reactions to various stimuli such as a sudden noise are recorded electrically. Dr. John L. Fuller testing a Basenji.

in groups of dogs but leadership is unimportant in most situations.

Critical Periods in the Development of Social Behavior

The study of the development of social behavior is essential to the study of the genetics of behavior since behavior of adults results from the interaction of heredity and early environment. It was found that the development of the social behavior of the dog could be divided into natural periods and that in one of these there is a metamorphosis of behavior almost as spectacular as the metamorphosis of form found in the tadpole and frog. These discoveries led to the hypothesis of critical periods:[20] namely that any period in which a new social relationship or a new type of social behavior appears is a critical one for determining future adjustment. Of particular interest is Fuller's[5] work on the capacity for the development of conditioned avoidance reflexes which appears abruptly at about 3 weeks of age. It has been concluded that one of the most important critical periods in the life of the dog begins at about this time.

Whether or not these results can be obtained in other species, it would appear that the dog offers vast possibilities for research on the effects of early experience in relation to mental health.

Individual differences in behavior which appear to have a genetic basis can be first recognized in the critical period described above and continue to appear with the development of new patterns of behavior. Thus, most of the genetic differences except those relating to reproduction appear to be present by 10 to 12 weeks of age. These interact with the environment in ways which may lead to either intensification or obliteration of differences.

The behavior of inexperienced animals is quite variable, and repeated experience and resulting habit formation lead to consistency. Thus, a difference which is at first only a greater frequency of one pattern of behavior over another may eventually lead to a habit of exhibiting only the preferred pattern of behavior.

Test Development

The development of suitable measures and tests of the variability of behavior in the dog proved to be a long and arduous task. Certain well known procedures such as the delayed response test[7] could be adapted to the dog, but in every case there was a problem of empirically working out techniques which were suitable to the species. It was also found that these tests had to be designed in relation to each other and to the age of the animals, each test more or less depending on the training which went before it. These tests have been described in a mimeographed manual[19]. The battery includes four types of tests: 1) performance and training tests such as manipulation, delayed response, and retrieving, 2) social behavior tests such as dominance and reaction to handling, 3) stress tests such as cage confinement and emotional reactivity[2], and 4) biological tests including physiological measures and somatotyping.

Two schemes were used to pick out important differences in behavior. One of these was based on the analysis of social situations. Tests were done chiefly in two social relationships: that between the handler and the dog and that between the dog and his litter mates. Within these general situations an attempt was made to test as many different types of social behavior as possible and thus obtain a well rounded picture of the individual. Tests were developed for both overt behavior and the internal physiological expressions of emotional arousal.

The second scheme for picking out important situations is Fuller's situational analysis[8], which is essentially a scheme for analyzing a situation according to the difficulties of adaptation for the organism. These are presumed to be dependent upon three kinds of interactions with the environment: directive interactions which result in stimulation and motivation, effective interactions, which are determined by the physical difficulties to be overcome, and cybernetic interactions which have to do with the complexity of the problem to be solved. It is believed that this scheme has a wide application in comparative psychology.

Certain of the tests have been described and a preliminary factorial analysis[14] has been made of a group of tests having to do with social and emotional behavior. The results indicate that the variability of the external emotional expression connected with agonistic behavior and particularly of the sort which may be described as fearful behavior has nothing to do with the variability in the internal expression of the same emotions. In short, an animal which may show little external manifestation of emotion may be undergoing an intense internal disturbance. The same results indicate that there is a tendency for sensitivity to sound which may be related to gun-shyness in dogs, and so on.

Analysis of Differences Within and Between Breed Populations

As a background study for experiments on heredity and behavior, a program of checking and verifying the existence of genes thought to influence coat color and texture has been undertaken, partly through breeding experiments, and partly through information provided by members of the American Kennel Club. Good evidence has been obtained for the existence of at least 13 genes in nine loci, and there appear to be two independent genes for red coat color[13].

Behavioral measurements on the breed popu-

lations which will form the parental generation of the cross-breeding experiments are now being analyzed[18]. Substantial numbers of Basenjis, Beagles, Cocker Spaniels and Wire-haired Terriers have been studied, and it is hoped that Shetland Sheepdogs will shortly be added to this list. The populations studied are not necessarily truly representatives of their respective breeds, although some attempt was made to secure "typical" animals as foundation stock. In general, most characters show large average differences between the breeds, but there is much individual variability within each population as well as considerable overlap.

More specifically considered[17], a study of the development of the social relationship between handler and puppy showed that certain individuals and populations tend to exhibit a great deal of escape and avoidance behavior at first, gradually becoming tamer, while others show strong positive responses from the first. On the other hand, when gently repressive handling was used to train puppies to stand still while being weighed, their originally variable behavior became fixed and consistent through habit formation, so that differences increased with the age of the animals.

A test involving a series of complex barriers showed rather slight differences between populations. In general, it has been found that it is very easy to find differences between populations which can be attributed to peripheral, emotional, motivational and physiological processes, and very difficult to find differences which might be called strictly "mental." However, large individual differences in performance on complex problems are found within populations. Whether or not these are genetic is a question requiring further analysis.

It is too early to make final conclusions, but the indications are that the special breed abilities for retrieving, herding[10], etc., are combinations of many independently variable traits (among which emotional and motivational characteristics are usually prominent), rather than complex behavior patterns which are inherited as such.

In addition to the observations on behavior, anatomical and physiological measurements are taken of each animal. The anatomical studies are not intensive, but are designed to test the hypothesis that body type is correlated with behavior. Several physiological measurements on five pure breeds have been analyzed[4], and each of the variables chosen was found to differ significantly between breeds. The characters studied included systolic blood pressure, arrhythmia of the heart beat, heart rate, resting pupil diameter, maximal pupillary contraction, and body temperature.

An obvious genetic difference is found between the sexes. This is reflected most clearly in behavior in patterns of courtship, though even here there is some overlap between males and females. In other tests, significant sex differences have thus far been found in only two cases. There is a slight, but reliable, tendency for the body temperature of males of a given breed to average 0.2°F. higher than that of females. A peculiar differential effect of weight on social dominance in the two sexes has also been established. Dominance in female-female pairings does not seem to be affected by weight, but in male-male and male-female pairings the heavier animal (excess of 8 percent or more) is usually dominant.

Paralleling the work with dogs, a program of studies on the inheritance of behavior in mice has been carried out[1]. Mice are particularly suitable for experiments requiring large numbers, since space and time requirements per individual are relatively small. Research has centered around the inheritance of susceptibility to audiogenic seizures. A marked strain difference between the dilute brown strain and the C57 blacks was reported by Hall in 1947[11]. Vicari[21] extended this study to other strains. The difference in susceptibility was at first attributed to a single gene difference[12], but later studies[6] suggest that multiple factors are involved, and that what appears to be a character of alternative expression is in reality a continuously distributed character of a quantitative nature. This trait has been used as test material for studies of physiological genetics, and Ginsburg[9] has postulated that susceptibility may be due to a gene controlled deficiency in the enzyme system regulating carbohydrate metabolism. Fuller[8] has found evidence that genes control critical time constants in the nervous system, and thus produce or suppress the tendency for convulsions to occur under strong stimulation.

Future Work

Only a small part of the data on sex and population differences in dogs has been analyzed to date, and work on this part of the project is proceeding as rapidly as possible. The experiment on cross-fostering is not yet complete, but the indications are that the effects on most characteristics are relatively slight.

The cross-breeding part of the program has just begun, and the first hybrids between Cocker Spaniels and Basenjis were born early in 1951. These two breeds probably show a greater number of extreme differences than any other two studied so far, and it is planned to obtain F_1 populations from reciprocal crosses and to backcross these to the pure breeds, so that F_1 and backcross litters can be raised by the same mothers, thus keeping the maternal environment constant.

An interesting part of the analysis of

the crossbreeding program will be a study of the correlation between various traits to see, for example, whether or not temperamental and emotional characteristics affect performance tests and whether or not physical and physiological traits are associated with behavioral ones. It is anticipated that the results may throw some light on certain general problems of education and personality differences.

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OLD CORN: NEW BOTTLE

THE fifth edition of this volume is a complete revision by J. J. Newlin, Edgar Anderson and Earl N. Bressman. This reviewer was familiar with the first edition, even before its publication, but has not seen the second, third and fourth editions. Accordingly he does not know in which editions the various changes have occurred but feels that many of them have been far from beneficial.

Neither this book nor a detailed review of it would be of interest to the members of the American Genetic Association. It is definitely elementary or less, in spite of the fact that some of the contents would be well above the heads of elementary students.

The order of presentation has been entirely changed from the logical sequence of the first edition to a sequence little better than chaotic. An example is in chapter 21, "Feeding and Marketing Corn." Here, after sections on the livestock use of corn, selling corn as grain, market grades of corn, and the corn loan program, one finds a section on "Soft Corn," which includes cribbing soft corn, shelling soft corn, the feeding value of soft corn, soft corn fodder and silage. This, in spite of the fact that there already has been a chapter on corn for fodder and silage.

One might expect to find under the title of chapter 20, "Harvesting the Crop," something pertaining to husking, cutting, shredding, or what have you. Actually, however, it contains only five sub-headings which pertain solely to corn cribs and elevators. More than 90 percent of the total corn crop is harvested as ear corn, yet this new edition only discusses harvesting ear corn in the chapter on harvesting hybrid seed corn.

*Wallace, Henry A., and Earl N. Bressman, *Corn and Corn Growing.* Fifth edition, revised by J. J. Newlin, Edgar Anderson and Earl N. Bressman. New York, John Wiley & Sons, Inc., 1949. 424 pages. Price, $4.50.

The first edition was utilized to emphasize the relation of weather to corn production and two of Henry Wallace's main interests: (a) the relation of weather to corn production, and (b) certain economic relations, particularly between price and yield and between corn and hog prices. These relations are important and previously had been largely overlooked in corn publications. The space devoted to these elements in the first edition has been reduced, though not disastrously. On the other hand, opportunity has been taken to emphasize certain interests of the present revisers. One may guess that Dr. Anderson is responsible for the statement that "one of the reasons that hybrid corn has been so successful is because it developed from such a wide and relatively recent mixture of corn, and many of the problems encountered in northern hybrid corn breeding are more closely related to this history than has been generally realized." An interesting opinion, but scarcely appropriate in a primer.

Some of the commercial hybrid seed companies whose corns have not performed well in official state tests have attempted (in part successfully) to spread the idea that such tests are not conclusive. One wonders whether revisor Newlin's interests (he is vice president of the Pioneer Hi-Bred Corn Company) influence the statement on page 196 that, "A man who grows corn to feed livestock or market has ceased to be greatly interested in the results of the scientific yield test. This same man is distinctly interested in a strip corn test on corn on his neighbor's farm. . . . Perhaps the corn growers . . . are more nearly right in giving their attention to larger fields, rather than . . . comparisons of corn in a scientific test." This point of view may help to sell corn hybrids that are inferior by scientific tests. Whether it is a good doctrine to teach vocational agricultural students, is another matter.

The large list of genetic characters included in the first edition is almost eliminated (and to advantage) in the fifth edition. This is offset by a 14-page list of "Corn Products and Their Uses" in chapter 27. Here several hundred items are hardly more than listed, one to a line. Some of the products and uses are self-explanatory, but others are meaningless in the absence of further explanation. Certainly it seems that such a list might well be replaced by ten pages describing some of the really important uses of corn and corn products.

Redundancy and actual errors occur here and there. Examples of the former are (p. 14), "Previously one man could care for about 40 acres before the coming of the tractor," and (p. 16), "The per capita consumption of corn eaten as human food is approximately 65 pounds annually." While not important, such diction adds nothing to the stature of the book and certainly sets a poor example for students at the high school level. One might expect that authors writing a book on corn would know the difference between stalks and stocks. Yet we find the latter in place of the former twice in the caption for figure 44. Again, (p. 37) since when has the term backcross "come to include also the selfing of the plants so produced."? Or, why, after discussing corn in Argentina and Mexico is a section needed on corn in "Latin America?"

Insofar as the discusion of corn growing is concerned, the title of the book might better have been restricted to "in the Corn Belt." In one chapter, brief mention is made of corn in the cotton states and in various other localities. The book, however, would have little value for students of agriculture outside the corn belt — and little of interest except for amusement at some of the statements made.

But enough. The price of the book is $4.50. And this reviewer feels that money spent for a copy of some recent more general book on crop production would be a better investment for students at any level. Some of the items on corn contained in *Corn and Corn Growing* would not be found in the more general volumes. The really important information necessary to an understanding of corn production would be presented, and much more effectively.

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THE SUGARCANES OF INDIA

Some Cyto-genetic Considerations

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THE sugarcanes grown in India fall into two distinct types; the thin canes and the thick or the 'Noble' canes. The thin canes are sub-tropical in their distribution and were widely cultivated in North India prior to the introduction of the so-called "Co. canes;" developed at the Coimbatore station. The 'Noble' canes are cultivated to a large extent in the tropical belt of India. Nearly 80 percent of the total four-million acres of sugarcane area of the Indian subcontinent is in North India. It is no wonder, therefore, that these thin sub-tropical canes were called the indigenous canes and by "Indian Canes" these alone were meant. The 'Noble' canes were considered to be a later introduction. Botanically these two types of canes fall into three distinct species of *Saccharum*. Barber[1] in his classical work on the thin canes (indigenous canes) recognized five groups: (1) Mungo, (2) Saretha, (3) Sunnabile, (4) Nargori, and (5) Pansahi; of these, the first four were placed by Jeswiet [14] under *S. Barberi* and the fifth was put in the species *S. sinense*. The 'Noble' canes belong to *S. officinarum*.

The exact origin of the cultivated forms is not fully understood. So far as the cultivated forms in India are concerned, the general belief is that the sub-tropical North Indian thin canes are the indigenous ones, and that the tropical canes were later introductions by one Captain Dick about the year 1827. Cyto-genetical studies at this Station have, however, indicated the possibility of the origin of the so-called indigenous canes from a promiscuous hybridization between *S. officinarum* and *S. spontaneum*.[16] On this basis *S. officinarum* must have been under cultivation in peninsular India from early times. They might have gone out of cultivation due to the attack of some disease to which they are susceptible; and their importation by Captain Dick in 1827 was very likely a reintroduction. In arriving at this conclusion several interesting cyto-genetical features have been taken into account.

Polyploidy in Sugarcanes

Cytologically all the known species of sugarcanes are polyploids having several sets of the basic number of 10 chromosomes. *S. officinarum* is an octoploid having $2n = 80$ chromosomes. The simple diploid forms with 20 somatic chromosomes are yet unknown. The lowest number known is in the form Tanangge, $2n = 60$, whose exact constitution is still a matter of controversy. On account of the high polyploidy and heterozygosity there is a wide range of variation even in selfed progeny. Also most of the seedlings of the selfed progeny do not survive, presumably due to the presence of a large reserve of lethal recessive genes in the genetic constitution of *S. officinarum* which, but for vegetative propagation, might have been the cause of the total extinction of the cultivated forms. For the same reason the exact nature and segregation of the hereditary factors cannot be worked out. The few attempts at inbreeding made at this Station proved—as the above discussion might suggest—the futility of adopting this as a means of improving sugar cane. For instance, seedlings on a large scale were raised from the selfed arrows of *S. Barberi*.[22] None of these represented a real improvement over the parents.

The results from inbreeding proving so limited that interspecific and intergeneric hybridization have been resorted to for breeding improved canes. It is now widely known how the Coimbatore Station was able to get a commercial seedling, Co. 205, by deliberately using *S. spontaneum* as the male parent. The use of these hybrids in a further breeding program mainly consisted of backcrossing these with *S. officinarum* (Nobilization) in

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OLD AND NEW SUGARCANES

Figure 16

At left is shown a planting of the improved variety CO 419, compared with the noble cane (*S. officinarum*) now grown to a large extent in the tropical zone of India.

order to lessen the undesirable characters like impurities in the juice which were imparted by the *S. spontaneum* parent along with such desirable characters as vigor and disease resistance.

The ease with which interspecific and even intergeneric hybridization is rendered possible in sugarcane is due, in no small measure to its high polyploidy. By itself it is a condition favorable for wide crossability by making autosyndesis almost the rule: namely, the internal pairing of the chromosomes derived from either parent, among themselves. This is because sugarcane is an allopolyploid. Consequently, even though the parental forms are not closely related, sterility does not always occur. While this phenomenon is useful in this respect, it is at the same time the despair of the breeder inasmuch as in a cross, synapsis seldom takes place between the two parental sets of chromosomes. The genetical outcome of this is obvious. Variations giving the parental combinations and their Mendelian segregation are almost impossible. No prediction can be made as to what will result from any particular cross. The high polyploidy, heterozygosity and autosyndesis all combine to make the chances of the reappearance of a particular synthesised variety almost impossible. It may be likened to a card game in which the number of cards dealt each player runs into hundreds. After a particular deal each person gets a large number of cards in a particular combination. An association of all these combinations produces a particular 'effect.' The chances that we can repeat this effect by getting the same combination a second time are almost nil.

Search for the Basic Genome

There are further complications. In a particular cross hundreds of genes in the parental forms have entered into a particular type of association *among* themselves (on account of autosyndesis) and *not between* themselves due to lack of synapsis between the parental chromosomes. It is almost impossible to get the same pattern of association involving all the hundreds of genes distributed over so large a number of chromosomes. Thus in 1916, forty plants of the F_1 generation of *S. officinarum* × *S. spontaneum* yielded in Co. 205, a cane of commercial value, that was immediately released for cultivation.[1] This identical cross was repeated for a number of years and though many thousands of F_1 seedlings were raised, not even a single repetition of Co. 205 or an improved form thereof was recovered.[22] This high allopolyploidy and the consequent autosyndesis being such a great handicap to the plant breeder, an effort was made at this Station by Parthasarathy,[18] to reduce the chromosome number to its basic complement. This was based on his suggestion[16] that generally the genetic or family relationship is close when reduced gametes function, but when the relationship is distant the compatibility of the cross is due to the functioning of unreduced gametes. The procedure adopted was to successively backcross *S. officinarum*, var. Vellai ($2n = 80$) to a closely related genus *Sclerostachya*, ($2n = 30$). It was found that in the first cross with *Sclerostachya*, reduced egg gametes functioned on the *officinarum* side implying a possible close relationship between *S. officinarum* and *Sclerostachya*.

Why, in the first backcross unreduced eggs functioned is not known. But in the second and third backcrosses reduced gametes functioned and in the latter where the chromosome number had been reduced to 40, the meiotic configuration consisted of 20 bodies made up of five trivalents, ten bivalents and five univalents. Of these $2n = 40$ chromosomes, 10 belong to *S. officinarum* and 30 to *Sclerostachya*. That means that the number of *S. officinarum* chromosomes has been reduced to its basic complement, $x = 10$. These ten chromosomes, if they had no homology with *Sclerostachya* should have remained as ten univalents, and the 30 *Sclerostachya* should have been organized into 15 bivalents. Instead, it was found that five of the ten *S. officinarum* chromosomes had paired with five *Sclerostachya* bivalents forming five trivalents. The other five *S. officinarum* chromosomes remained as univalents. The rest of the *Sclerostachya* chromosomes formed ten bivalents. This grouping indicates that the basic complement of ten *officinarum* chromosomes contains five chromosomes homologous to *Sclerostachya*.

In an effort to determine the homology of the remaining five chromosomes, the backcrossed progeny ($2n = 50$) was crossed this year with another closely related genus *Narenga* ($2n = 30$). The seedlings are now in the First Ground Nursery, and a few of them are in the short blade stage. An examination of the pollen mother cells in acetocarmine smears has revealed the presence of 18 to 20 bodies, four or five of which are much bigger than the rest. The backcrossed progeny contains $2n = 50$ chromosomes of which 20 are *S. officinarum* and 30 are *Sclerostachya* chromosomes. In meiosis it forms 25 bivalents; ten bivalents of *S. officinarum* plus 15 bivalents of *Sclerostachya*. This has been crossed with *Narenga* ($2n = 30$). If the ten *S. officinarum* chromosomes held no homology with *Narenga* chromosomes, the meiotic configuration in the cross should show 25 bodies, namely ten univalents of *S. officinarum* and 15 bivalents made up of *Sclerostachya* and *Narenga* chromosomes. This is on the assumption that *Narenga* and *Sclerostachya* chromosomes are near enough to pair with one another. There is justification for this assumption inasmuch as in a cross between *Narenga* and *Sclerostachya*[17] the F_1 hybrid showed $2n = 30$, indicating that reduced gametes had operated. This could not have happened, but for their compatibility. The other alternative is that all

of the 40 chromosomes (ten *officinarum* plus 15 *Sclerostachya* plus 15 *Narenga* = 40) should remain as univalents, resulting in complete sterility. However, the unmistakable presence of what appears to be trivalents and the total number of bodies being 18 to 20, indicates the possibility that five of the basic chromosomes of *S. officinarum*, which were established to be components of *Sclerostachya*, also showed homology with *Narenga* chromosomes.

The fact that *Sclerostachya* and *Narenga* cross easily, with complete pairing of chromosomes, need not automatically lead to the expectation that in a cross with the backcrossed progeny, the basic chromosomes of *S. officinarum* which were shown to be a component of *Sclerostachya* would also show the same relationship with reference to *Narenga*. It is quite conceivable that both the two sets of five basic chromosomes of *S. officinarum* may be components of *Narenga*, in which case the meiotic configuration in the cross may be expected to be ten trivalents (O.-S.-N.) plus five bivalents (S.N.). On that hypothesis the three genera involved must have originated from a common putative ancestor, five of whose chromosomes are common to all three, the other five being common only to *Narenga* and *Saccharum*, but not to *Sclerostachya*. But as the configuration obtained is, (as has already been explained) a total of about 20 bodies, all that can be said pending further investigation is that all three genera, *Saccharum*, *Sclerostachya* and *Narenga* may have had a common origin in respect to these five chromosomes.

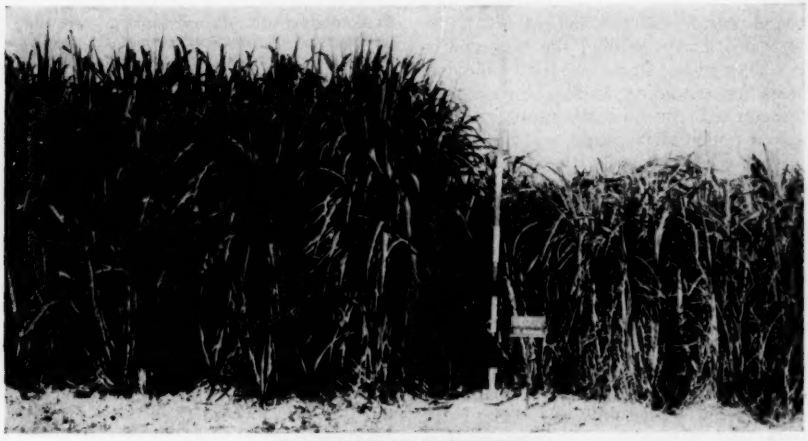
Other Generic Crosses

In addition to employing *officinarum* × *Sclerostachya*, backcrossed progeny (in whose gametic cells, the *officinarum* chromosomes are reduced to their basic number) for crossing with *Narenga* and *Erianthus* (*ravennae*), a series of *officinarum* × *Narenga* and *officinarum* × *Erianthus* backcrosses are being made, for the purpose of determining the homology of the other five chromosomes in the basic complement of ten *officinarum* chromosomes. It is worth remembering in this connection that the proximity between *officinarum* and *Narenga* can also be inferred from the fact that in the cross *S. officinarum* var. Vellai ($2n = 80$) × *Narenga* ($2n = 30$) made by Barber[1] it was found that the reduced egg gamete has functioned on the *officinarum* side.[10]

There is another recently-discovered important character through which relationship between *S. officinarum*, *Sclerostachya* and *Narenga* would appear to be indicated. Investigations at this Station[6] have shown that the presence or absence of starch in the internodal cells of the different species of *Saccharum* and related genera, is not a haphazard phenomenon, but one of taxonomic importance. *S. officinarum* has no starch; nor do *Sclerostachya* and *Narenga*. This feature shared by these three would appear to lend support to the view that they are closely related genetically. At the same time it has to be remembered that *S. officinarum* when crossed with other genera like *Sorghum*, *Zea Mays* and *Erianthus*, behaves in the same manner as it does with *Narenga*, that is, the reduced egg gametes are functional.[20,10,11] To elucidate this point, *Sorghum Durra*, Stapf, *Sorghum halepense*, and *Zea Mays* were crossed with the 50-chromosome *S. officinarum* × *Sclerostachya* backcrossed progeny, in the same manner in which *Narenga* was crossed. It was found, however, that in all these cases only 25 bodies were formed during Metaphase I, that is, ten *S. officinarum* bivalents plus 15 *Sclerostachya* bivalents. Obviously the pollen has not functioned in the cross; whether they are selfed progeny or parthenogenetic derivatives could be determined only by a study of the megasporogenesis. Thus an interesting situation has arisen in that, while in a cross with these genera, *Sorghum Durra*, *Sorghum halepense* and *Zea Mays* a reduced egg gamete on *S. officinarum* side has functioned, it is found that when *S. officinarum* chromosomes are reduced to their basic number they show no pairing affinity.

On the basis of the suggestion of Parthasarathy[16] already referred to, *Sorghum*, *Zea* and even *Bambusa* (in which cross also reduced gametes are known to function[12]), should be regarded as being genetically related to *S. officinarum*. *Prima facie* this may look a bit unnatural especially when it is remembered that on this interpretation, a species which may be regarded as closely related, namely, *S. spontaneum*, would have to be relegated to a distant position, inasmuch as in a *S. spontaneum* cross it is always the diploid egg that functions on the *officinarum* side. Either the suggestion is wrong or we should not be unduly perturbed at such seemingly glaring unlikelihoods which emerge out of this interpretation. For instance, has not *Sclerostachya* been established to have an affinity with *officinarum*, which it has not been possible for *spontaneum* to exhibit? Even so, it may well be that these seemingly distant genera do show some amount of relationship, although not ancestral, in the sense that they may not have had a common origin as revealed by their chromosomes showing no homology to the *officinarum* chromosomes when the latter are reduced to their basic number.

In this short review the several crossing results gathered at the Station are presented and sought to be interpreted mainly on the basis of the above mentioned suggestion. Difficulties encountered in establishing interrelationships on this criterion are also presented and in some cases suggestions have been offered to explain them.



SUBTROPICAL VARIETIES

Figure 17

Plantings of an "indiginous" northern Indian thin cane compared with the improved variety CO 213, which replaced it.

Experiments at the Coimbatore Station

Of the several interesting cytogenetic features, the most important is, as has already been mentioned, the capacity of sugarcane to produce the reduced and unreduced type of egg gametes. The contribution of the diploid number by the pistillate parent was first noticed by Bremer in 1923, in natural hybrids between *S. officinarum* var. Zwart Cheribon ($n = 40$) and *S. spontaneum* var., Glagah ($n = 56$). The same feature was observed at the Coimbatore Station in crosses between *S. officinarum*, var., Vellai ($n = 40$) and *S. spontaneum*, Coimbatore, ($n = 32$) by Dutt and Subba Rao.[5] Triploids have also been found to occur among selfed progenies and intra-specific hybrids of *S. spontaneum*.[9]

It was Narayanaswamy who actually found out the mechanism by which the doubling of the chromosomes took place in the pistillate parent.[15] Bremer[3] considered this doubling to be a phenomenon associated with interspecific hybridization in *Saccharum*, the doubling having occurred in the egg cell during fertilization. Narayanaswamy, working on the megasporogenesis of *S. officinarum* and *S. spontaneum*, found a fusion of the two inner megaspore nuclei to give rise to diploid megaspores, this phenomenon being more frequent in *S. officinarum* than in *S. spontaneum*. Unlike other cases of diploid egg formation through such means as absence of pairing, double division of univalents and suppression of first division, the method found in sugarcane seems to be unique. Being a post-meiotic phenomenon its genetic consequence is also important in the extreme. For instance, parthenogenetic derivatives from diploid eggs of such origin show a wide range of variation which would not be possible if the egg had attained its diploid condition by the ordinary means. At this Station such parthenogenetic seedlings were obtained by Janaki Ammal.[13] The seedlings showed variation in sucrose content, fertility, etc.

Besides the formation of diploid gametes some varieties have the capacity to give rise to gametes with chromosome number quite different from its own haploid or diploid number. Such a behavior was observed by Bremer[4] in the variety POJ.100, which when crossed with Kassoer gave rise to seedlings having $2n = 152$, 157, and 148 chromosomes. He attributed this to the unbal-

anced nature of the hybrid POJ.100. Subramaniam[21] studied the megasporogenesis and has furnished the cytological basis for obtaining seedlings with such unexpected chromosome numbers. Co. 421, a pollen sterile cane, when selfed as well as when crossed with *Coix* or *Bambusa* gave rise to two kinds of seedlings; one looking like the mother parent and having the same chromosome number, $n = 59$, — obviously these are parthenogenetic derivatives—and the other thin and having only $n = 43$ chromosomes. During first division the 59 bivalents arrange themselves into two groups at metaphase. The group on the equatorial region consists of 43 bivalents and the other lying above towards one of the poles had 16 bivalents. An egg cell having 43 chromosomes is formed; but this egg cell is found to be divided before fertilization. Absence of cell wall formation after chromosomal division would result in the doubling of chromosomes. Thus seedlings having $2n = 86$ are formed from such eggs. The resemblance of these thin seedlings to North Indian canes[16] suggested the probable origin of the North Indian canes. Co. 421 itself is a complex *S. officinarum* × *S. spontaneum* hybrid (POJ.2878 × Co.285). POJ.2878 has got the genes of both *S. officinarum*, var., Zw. Cheribon and *S. spontaneum* Glagah. Co.285 is a cross between *S. officinarum* var. Green sport and *S. spontaneum*, Coimbatore. Since a seedling resembling a North Indian cane was derived parthenogenetically from a form in whose constitution *S. officinarum* and *S. spontaneum* had entered, it is believed probable that the thin North Indian canes *S. Barberi* may have arisen by a promiscuous hybridization between *S. officinarum* and *S. spontaneum*.

A series of crosses are being made at this Station in order to gather more data likely to throw light on this question. Firstly, *Barberi* (Saretha $2n = 92$) has been crossed with *S. spontaneum* var. Coimbatore ($2n = 64$). This hybrid has to be successively backcrossed to *S. spontaneum*, which may be expected to reduce the *S. officinarum* chromosomes therein to their basic number. Similarly *S. Barberi*, var. Saretha ($2n = 92$) has been crossed with *S. officinarum* with a view to successive backcrossing with *S. officinarum*. This may be regarded as complementary to the previous series of backcrosses, in that it may be expected to reduce the *S. spontaneum* chromosomes to their basic number. These two series of backcrosses may throw some light on the constitution of *S. Barberi*.

In the meantime the chromosome numbers determined so far in interspecific crosses involving *S. officinarum*, *S. Barberi*, *S. robustum* and *S. spontaneum* would appear to give one an idea of the complexity of determining interrelationships among them. In the cross *S. Barberi* × *S. spontaneum* (Saretha $2n = 92$ and *spontaneum* $2n = 64$) the hybrid P.3146 has shown $2n = 78$ to 80 chromosomes.[19] Obviously reduced gametes have entered into the cross. Investigations at this Station have shown that this non-reduction[15] on the egg side results from the fusion of two haploid nuclei of the spore tetrad. Whether this is universal among all species of *Saccharum* remains yet to be determined. Narayanaswamy's findings were that this was more common in *S. officinarum* than in *S. spontaneum*. Nothing is known so far of the same phenomenon in *S. Barberi* and *S. robustum*; nor is it very clear whether the functioning of the diploid gametes is confined only to the egg side of *S. officinarum*. In the cross *S. officinarum*, var. Vellai, ($2n = 80$) × *S. spontaneum* ($2n = 64$) the hybrid Co.205 showed $2n = 112$, indicating the functioning of the diploid egg on the *S. officinarum* side. In the reciprocal cross *S. spontaneum* ($2n = 64$) × Zwart Cheribon (*S. officinarum* $2n = 80$) the chromosome number was also found to be $2n = 112$ in the hybrid,[19] implying functioning of diploid male gametes on the *S. officinarum* side. The numbers in the reciprocal crosses involving local varieties of *S. officinarum* like Chittan, Kaludai Boothan etc., are being determined. But it seems likely that the unreduced condition need not be restricted to the egg gamete of *S. officinarum*, but that its pollen gamete also may function as a diploid when *S. officinarum* is used as a pollinating parent.

In the cross *S. Barberi*, var. (Saretha $2n = 92$) × *S. spontaneum*, Coimbatore ($2n = 64$), since reduced gametes have functioned it may be taken as an indication of the close relationship between the two. But in the cross made at this Station between *S. officinarum*, var. K. Boothan ($2n = 80$) and *S. Barberi*, var. Saretha ($2n = 92$) the hybrid S.G.377/I, shows $2n = 122$ to 126 chromosomes[19] confirming the observation of Brandes,[2] that in such a cross between *S. officinarum* and *S. Barberi* or *S. sinense*, the monoploid chromosome number of the noble parent is doubled. If, as it is surmised,[16] *S. Barberi* contains both *S. spontaneum* and *S. officinarum* chromosomes, then *Barberi* with *spontaneum* or with *officinarum* should behave in the same manner, namely, the monoploid gametes should enter into the cross. The possible reason for this seemingly

contradictory behavior would appear to be that in *Barberi* there are more *S. spontaneum* chromosomes than *S. officinarum* chromosomes. Hence the probable proximity of *S. Barberi* to *S. spontaneum*. It is quite likely that if the number of *S. spontaneum* chromosomes increases beyond a certain limit, *S. officinarum* is disturbed and so begins to function as a diploid on its gametic side. That *S. officinarum* and *S. spontaneum* are genetically distant can be inferred from the fact that whenever *S. spontaneum* is used with *S. officinarum*, the latter always contributes unreduced egg gametes to the cross. So if in *Barberi* there are more *S. spontaneum* chromosomes than *S. officinarum* would relish, presumably it at once functions as a diploid. But if the number of *S. spontaneum* chromosomes is considerably reduced *S. officinarum* is not presumably disturbed by their presence and would function with its monoploid egg gametes.

This behavior of *S. officinarum* is easily seen in the successive series of Nobilization. In the Java series of Nobilization the *S. spontaneum* chromosomes go on decreasing from 112 in Glagah to 14 in POJ.2725 in the third Nobilization stage. In the first two stages of Nobilization where 56 and 28 *spontaneum* chromosomes, respectively, are present (in Kassoer and POJ.2364) it is found that the diploid egg functions on the side of *S. officinarum*. But in the third stage of Nobilization where only 14 of the *S. spontaneum* chromosomes are functioning, the reduced gamete on the *S. officinarum* side is seen to function. Thus it would appear that when the proportion of *S. spontaneum* chromosomes to the total falls to about 15 to 20 percent, they cease to affect the *S. officinarum* complement, which consequently begins to function normally by contributing the haploid gamete.

At this Station we have also carried the Nobilization up to the second stage.* The third Nobilization is being carried on. The fact that *S. Barberi* and *S. spontaneum* behave alike in a cross with *S. officinarum* i.e. the functioning of the diploid gamete on the *S. officinarum* side may also be taken as an additional indication of the relationship between *S. Barberi* and *S. spontaneum*. It would appear that support for this interpretation could be had from the starch-content character exhibited by these species of *Saccharum*, to which reference has already been made.[6] There is no starch in *S. officinarum;* but there is starch in *S. spontaneum* and *S. Barberi*. If, as is believed likely, *S. Barberi* arose as a result of promiscuous hybridization between *S. officinarum* and *S. spontaneum*, then the presence of starch in *S. Barberi* would imply more of *S. spontaneum* blood than *S. officinarum* as the presence of Starch in a *spontaneum* character. And this is what has been revealed in a *S. Barberi* × *S. spontaneum* cross. On account of more *S. spontaneum* chromosomes being present in *S. Barberi*, reduced gametes have entered into the cross.

In a cross effected at this Station[19] between *S. officinarum* var. Vellai ($2n = 80$) × *S. robustum* ($2n = 72$) the F_1 hybrid (G.1680) has shown $2n = 76$. The *S. robustum* that we have at this Station came from New Guinea and shows a diploid chromosome number of 72 as against $2n = 84$ reported by Brandes.[2] Presumably there are different karyotypes in this species of *Saccharum*. Obviously in this cross the reduced gametes have functioned, implying a close relationship between *S. officinarum* and *S. robustum*. This is as it should be, for according to Grassl[8] *S. officinarum* arose from *S. robustum* in the New Guinea area. Also in the matter of starch content, both *S. officinarum* and *S. robustum* share the same feature of the absence of starch.[6]

It is also worth mentioning that according to Brandes[2], when a noble cane is crossed with *S. robustum* "there is an increase of chromosomes above the number which corresponds to the sum of the monoploid numbers of the parents, but it is considerably less than the sum of the diploid number of *S. officinarum* and monoploid number of *S. robustum*." Whether this is a case of functioning of egg gametes with unexpected chromosome numbers such as those derived from a cross between Co.421 and *S. officinarum* variety Poovan is not known.[21] But in the cross made here, reduced gametes have functioned. Brandes himself says "from a morphological point of view it (*robustum*) is much nearer to the Noble varieties than are the forms of *S. spontaneum*." This cross has confirmed Brandes' view.

In the cross *S. Barberi* (Saretha $2n = 92$) × *S. robustum* ($2n = 72$) the F_1 hybrid (P. 3134) showed $2n = 82$ (46 + 36) chromosomes,[19] which corresponds to the sum of the monoploid number of the parents. If *S. robustum* and *S. officinarum* are very close together then the behavior of *S. robustum* with *S. Barberi* should not be the same as that of *S. officinarum* with *S. Barberi*. In the latter cross an unreduced egg gamete on the *S. officinarum* side has functioned and this was interpreted as possibly being due to more *S. spontaneum* chromosomes being present in *S. Barberi* than *S. officinarum* chromosomes. But in the *S. Barberi* × *S. robustum* cross, only haploid gametes have functioned.

Two interpretations of this are possible. Firstly, it may be that *S. robustum* contains some chromosomes homologous to *S. spontaneum*. *S. Barberi* is suspected of containing more *S. spontaneum* chromosomes than *S. offi-*

**S. officinarum* var. K. Boothan ($2n = 80$) × *S. spontaneum*, Coimbatore, ($2n = 64$) = Hybrid A 10. This hybrid, $2n = 112$ (80 + 32), represents the 1st Nobilization. Chittan, $2n = 80 \times$ A 10 ($2n = 112$) = hybrid seedling ($2n = 136$) (2nd Nobilization).[19]

cinarum chromosomes for the reason that in *S. officinarum* × *S. Barberi* haploid gametes have functioned on the *S. officinarum* side, and in the cross *S. Barberi* × *S. spontaneum* reduced gametes have entered into the cross. On the basis of a homology between *S. robustum* and *S. Barberi* the origin of *S. officinarum* from *S. robustum* would not be tenable and so this is not likely to be the cause for the functioning of haploid gametes in the cross *S. Barberi* × *S. robustum*.

The other possibility is that this formation of two kinds of gametes, haploid and diploid, is confined mainly to *S. officinarum* and to a lesser extent to *S. spontaneum* and that *S. robustum* and *S. Barberi* may not show this phenomenon. In that case where only *S. officinarum* has figured in a particular cross can one make use of this criterion for purposes of establishing family relationships. Investigations are in progress at this Station to study in detail the megasporogenesis in all the species of *Saccharum* to find out in which of the species this phenomenon is present and in what proportion these diploid gametes are formed.

It would thus appear that the determination of the phylogenetic relationships between different species of *Saccharum* is fraught with considerable complexity. The various crosses and backcrosses that are being effected and the data that are being gathered in regard to the organization of the gametic cells may in time clear up problems of descent and interrelationship.

Summary

A short review has been given of the cytogenetical work that has been done at the Coimbatore Station, with an indication of the lines along which work is in progress and is being continued.

The work pertains to the constitution of *S. officinarum* and the determination of interrelationship among the various species of *Saccharum* and allied genera. An attempt has been made to interpret interspecific and intergeneric affinities on the basis of several interesting cytogenetical features.

The complexity of the problem of speciation in *Saccharum* has been pointed out with reference to some cytogenetical discrepancies which have been presented in the course of the review.

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A UNIQUE HERD OF HEREFORD CATTLE

The R. G. Gietz Herd Has an Average Inter-se Relationship Greater Than That Between Full Sibs

H. H. STONAKER*

IN a search for divergent sources of Hereford cattle to furnish foundation stock for developing inbred lines at the Colorado Agricultural Experiment Station, Dr. S. S. Wheeler of this station suggested that the R. G. Gietz herd near Laramie, Wyoming, might provide a useful nucleus for a line because of an unusual breeding program which had been followed since 1926. At that time, the Gietz herd was closed to outside sources of breeding animals and since then a program of purposeful close breeding has been in effect. The herd may be unique among Hereford herds in the United States in that no animal in it has any direct relationship to the most prominent ancestor in recent years, which, according to Willham,[4] was Prince Domino 499611. Also, as far as the author knows, there are no other American Hereford herds which have recently undergone such a prolonged period of close breeding as has been practiced in this herd. A Shorthorn herd was described by Lush[2] in which a somewhat similar breeding program was practiced.

As a student of genetics and breeding, Mr. Gietz became intrigued with the idea of establishing a strain of Hereford cattle which would be high in merit and have greater uniformity in their inheritance than is usual among purebred cattle. He decided that his most useful tool for accomplishing this would be a program of planned inbreeding, preferably with many half-sib and a few son-to-dam matings. This plan was begun on November 30, 1925, with the birth of a much admired bull calf, Bonnie Arden, 1454389, out of a cow which came to the ranch in a group purchased from the L. G. Davis and R. W. Taylor herd. Since that time there have been no additions to the herd which consisted of about 70 cows and three herd bulls at the time this study was made. Thus, the herd offered an interesting opportunity to evaluate how this genetic isolation from the rest of the breed affected the relationships among calves and the amount of gene fixation which probably took place. Also there was an opportunity to compare outward effects from this breeding program with those in herds more conventionally bred.

Methods

The analysis was based upon Wright's[5] methods of estimating relationship and inbreeding. This method has been widely used and often described and will not be discussed further here. Systematic methods for the calculation of inbreeding and relationship coefficients in herds have been described by Emik and Terrill.[1] The data consisted of the pedigrees of 43 bull and heifer calves which were born in the Gietz herd early in 1947, and for which applications for registration had been made by the summer of 1947. The pedigrees were completed to a base registration number 413606. This gave a base birth date between 1912-1914. It represents about five generations of cattle breeding. In all, 903 relationships between the 43 calves were calculated in addition to the inbreeding coefficients.

Results

In inbreeding, the 1947 calf crop averaged 30.7 percent with a standard deviation of 6.4 percent and a range in inbreeding coefficients between 19 and 47 percent. This would approach the inbreeding expected from six generations of matings in a closed two-sire herd. (Lush.[3])

The average inter-se relationship among the 1947 calves was 55 percent, with a standard deviation of four percent, and a range between 36 and 67 percent. This indicated that randomly selected calves from the herd averaged more alike genetically than full sibs.

Other than the rise in inbreeding and inter-se relationship coefficients resulting from this mating system, a high degree of relationship of present calves to Bonnie Arden had been maintained. Sons and daughters of Bonnie Arden formed exclusively the foundation of the present herd. In the 1947 calf crop, five generations after he was used, Bonnie Arden's relationship to the calves averaged 43 percent, almost as much as if he had been their sire. This genetic relationship was approximately fifteen times as great as that which occurs be-

*Colorado Agricultural Experiment Station, Scientific Series Article 354, Colorado A & M College.

GIETZ BULL

Figure 18

In this herd, with a coefficient of inbreeding of nearly 31 percent, a characteristic shape of head and conformation has been achieved. No serious abnormalities have been observed, and Gietz bulls have been used by other ranchers with marked success.

tween an animal and a single ancestor appearing but once in the fifth ancestral generation.

The degree of genetic isolation of the herd from the breed rested largely upon whether or not Bonnie Arden's ancestors were those which have been and are popular in the breed. By extending the pedigree of Bonnie Arden, it was possible to estimate the probable genetic likeness of this sire to the breed at the time of Willham's study[4] and provides evidence on how far from the breed this herd may have drifted as a result of the isolation.

Only the direct relationship was calculated as a means of estimating the nature of this genetic drift, but it was believed that it afforded a fair indication of the probable total relationships.

Table I compares the direct relationship of Bonnie Arden to the most prominent ancestors reported by Willham.[4]

It appeared, (Table I), that there was no great difference in the genetic background of the Gietz foundation sire and the breed until Anxiety 4th appeared. Bonnie Arden had almost twice as much direct relationship to Anxiety 4th, Don Carlos, Lamplighter, and Beau Donald as did the rest of the breed at that time. On the other hand, he had no direct relationship to Prince Domino, the most prominent recent ancestor, nor to Domino and Beau President. This probably makes the herd unique among United States herds for much of the relationship of present day animals to Anxiety 4th comes through Prince Domino. It is possible that this herd was as closely related to the long admired Anxiety 4th as any herd in existence, and yet it had completely circumvented a branch of the gene stream which the rest of the breed had followed in keeping this relationship to Anxiety 4th high. For instance, the two herd bulls calved in 1924 and 1925 in the Mousel Brothers' herd, long known for line-bred Anxiety 4th cattle, were on an average about the same in direct relationship to Anxiety 4th as was Bonnie Arden. These two bulls, Advance Domino 1381854, and Advance Mischief 1323063, were 21 and 12 percent directly related to Anxiety

TABLE I. Direct relationships between the Hereford breed (1930) and prominent ancestors as compared with relationship of Bonnie Arden to those ancestors.

	Breed in 1930	Bonnie Arden
Lord Wilton	.01	.01
Mars 12	.03	.02
Garfield	.01	.04
North Pole	.05	.05
Anxiety 4	.08	.17
Don Carlos	.08	.14
Beau Brummel	.10	.13
Lamplighter	.04	.05
Beau Donald	.02	.09
Beau President	.04	.00
Domino	.05	.00
Prince Domino	.07	.00

4th, as compared with Bonnie Arden's 17 percent.

Another interesting comparison existed between this and the Neal herd of Shorthorn cattle described by Lush.[2] Both herds, at the time of analysis, had been closed for approximately twenty years. The Gietz herd was considerably the larger of the two. Relationships of the calves in each herd to their foundation sires were almost identical. The Shorthorns were 42 percent related to Sultan's Banner, whereas, the Herefords were 43 percent related to Bonnie Arden. In inter-se relationship, the Herefords were somewhat higher than the Shorthorns—55 percent as compared with 43 percent. The contrast in inbreeding coefficients, however, showed that the systems have had different emphasis. In the Neal herd the inbreeding was 16.9 percent, whereas, in the Gietz herd, it was almost double that, or 30.7 percent. Lush[2] pointed out that the increased inbreeding in the Shorthorn herd was not a desired objective but a by-product of the system. On the other hand, Mr. Gietz has purposely increased the inbreeding in his herd beyond that which would necessarily occur in a closed herd of that size.

It was difficult to evaluate the phenotypic merit of the Gietz cattle as it may be related to the unusual breeding program followed. Weights, measurements or scores of the cattle have not been taken by which comparison with other herds might be measured. Because of different herd environments, such measures would probably lack value in describing genetic differences. The herd had not been developed with heavy levels of grain feeding. It probably classified as intermediate in body size and it appeared that there were certain distinguishing characteristics in the shape of the head and possibly other skeletal similarities. Abnormalities had been either rare or non-occurring. Slight deviations from the regularly accepted Hereford color patterns occasionally occurred. Whether these deviations were greater or fewer than those usually found is not known. The cattle were mostly of an intermediate shade of red, but variations in this characteristic also were apparent.

Performance in Other Herds

Most of the bulls from the herd go to commercial range cattlemen in Wyoming and Nebraska. Mr. Gietz supplies a limited number of bulls to a rather steady clientele, with frequent repeat orders. They are sold in relatively thin condition at moderate prices. A nearby rancher, Otto Dreyer, has used nothing but Gietz bulls for twenty years on his range herd. Dreyer cattle have long been sought by feeders and have the reputation of selling for a higher price per pound than is generally received by neighboring ranches for cattle of similar ages. The Dreyer cattle have been contracted exclusively by one Yale, Iowa, feeder, the late Stanley Thompson, for a period of 24 years, and Amos Siglund of Seymour, Iowa, for eleven years. Mr. Dreyer is of the opinion that his range herd has been improved in quality as a result of the close breeding which has been used in producing the Gietz bulls.

Summary

The breeding of the R. G. Gietz herd of Hereford cattle at Laramie, Wyoming, which has been closed to outside breeding since 1926, has been described. The average inter-se relationship among 1947 calves was 55 percent, higher than that between full sibs. The average of the inbreeding coefficients was 30 percent. The herd is unusual in that it is based upon Anxiety 4th ancestry but has completely circumvented Prince Domino, a sire which is prevalent in pedigrees of the Hereford breed in the United States and through which much of the relationship to Anxiety 4th is commonly retained. The herd is of intermediate size and shows considerable phenotypic uniformity. Surplus bull calves were sold into range cattle herds where they have a reputation for siring high quality feeder cattle.

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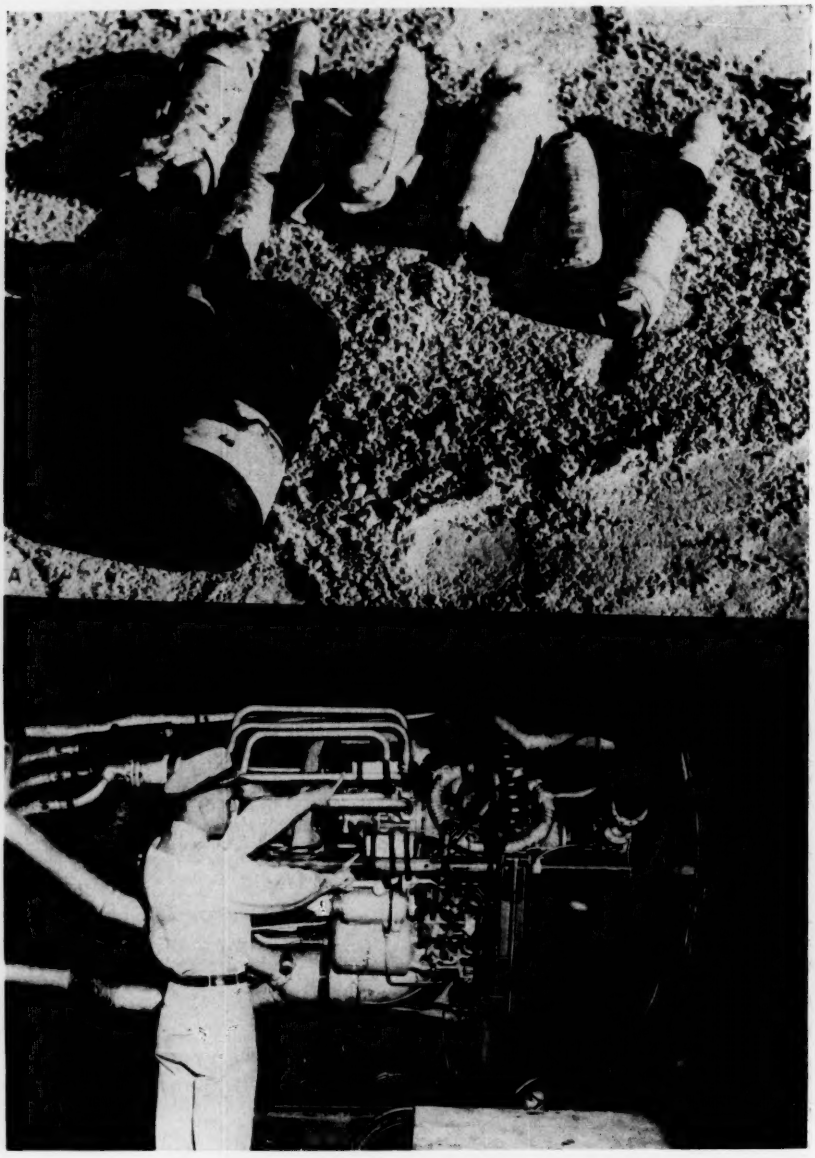


SEED SAMPLES FOR STRATOSPHERE EXPOSURE

Figure 19

A—shows seed samples in wrapped containers ready to be placed in rocket. *B*—shows the method of placing the containers in one section of rocket prior to flight. The junior author is pointing to the containers tied in place. The thin sheet-metal outer covering of the rocket was placed over the containers before the takeoff.

A STUDY OF GENETIC EFFECTS OF COSMIC RADIATION

On Cotton Seed

GOVAN N. STROMAN AND THOMAS H. LEWIS*

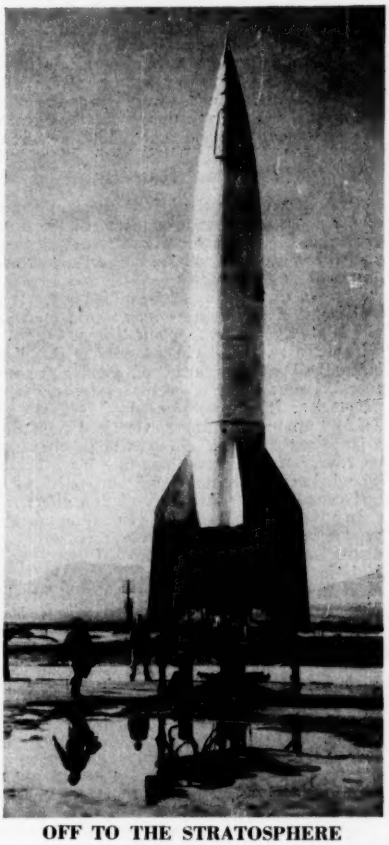
IN contrast to the great body of information available on the biological effects of radiant energy of most frequencies, very little is known of the possible action of the components of cosmic radiation on living tissues. The relatively few published studies, taken as a whole, are inconclusive, and in some instances contradictory.[1,2,3]

Experimental work has been discouraged physically by the difficulty of access to the upper atmosphere at levels of the primary component, and theoretically, by the known low intensity of the total radiation. One does not expect detectable effects from 15 milliroentgens/day (70,000 ft.) when doses in hundreds or thousands of roentgen units are commonly used in similar laboratory assays. The discovery, in the radiation incident to our atmosphere shell, of tremendously energetic heavy nuclei capable of great penetration and high specific ionization makes new investigation desirable. Since absorption of these particles and dissipation of their energy is accomplished very rapidly by air molecules, little may be learned by shielding experiments or by exposures on mountain tops or in aircraft. Further, roentgen units may not express with accuracy the tissue ionization by absorption of quanta from extremely heterogenous radiation.

Very recently it has become possible to test directly the natural radiation of the stratosphere above 85,000 feet by means of high altitude sounding rockets and balloons. We have used these vehicles for carrying small heat and impact resistant containers high above the earth. Although test materials have been varied, this report will deal only with certain cotton seed samples which have been grown through the second generation.

Material and Methods

For the initial experiments, seed were selected from three individual plants of a strain segregating for certain seedling characteristics. The dormant seed were exposed November 18, 1948 in a V-2 rocket which ascended to 90.5 miles during a 595.5 second flight. The seeds from plants 7412-36 and 7412-40 were enclosed in a duraluminum container with walls 1 mm. thick. Seed from plant 7412-30



OFF TO THE STRATOSPHERE

Figure 20

V-2 rockt ready for flight into the upper stratosphere. During such a flight, lasting less than eleven mintes, a height of nearly 100 miles was reached.

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were placed in a non-metallic rigid plastic tube (polystyrene) with 5 mm. walls. Both containers were fastened to the framework of the rocket and were covered only by a thin (0.025 inch) sheet metal outer skin.

After recovery of the rocket and the sample containers, the seed were planted in rows in the greenhouse. Alternate rows were planted with control seed from the same parent plant. The plants were measured on February 2, 1949 and April 26, 1949. When the cotton from the plants was ginned, record was made of percent lint, lint index, boll weight, yield, and percent of 1⅛ inch plus fibers.[4,5,6]

Greenhouse plantings were also made of second generation seed with alternate rows planted to controls. Counts were made on the seedlings for the contrasting phenotypes green or light-green cotyledon, and yellow leaf edge.

Data and Results

Table I compares the height and boll count of the exposed and control plants of the first generation. The differences are not significant statistically and the apparent increases demonstrated in the exposed 7412-30 and 7412-36 plants are reversed by those of 7412-40. The boll count simply reflects increase in number of bolls with increased plant height.

Table II A, B and C show percent lint, lint index, boll weight, calculated yield and percent 1⅛ plus fibers of plants of the exposed generation. The exposed seed of 7412-30 and 7412-40 produced a higher calculated yield and a large percentage of 1⅛ plus fibers than the controls, but the reverse was true for 7412-36. The differences are not significant statistically, and cannot be ascribed to radiation effects.

In the test of second generation plants grown in the greenhouse, the percentage of plants with cotyledon yellow-leaf edges was high in the exposed group (Table III). A more extensive field planting counted for six phenotypes gave low totals for yellow leaf edge in both exposed and control plants (Table IV), indicating an extraneous mutagenic agent not associated with high altitude radiation, and negating the significance of the differences in Table III. The germination of the second generation of exposed seed was low in the field, especially in the progeny of plant 7412-36 (Table IV). The percentage of plants with light-green cotyledons was high in the progeny of planted 7412-40, but low in 7412-30 and 7412-36.

TABLE I. Comparison of plant stature and boll count on three pregonies and their controls.

Plant number	Number of plants	Height in cm., Feb. 2, 1949	Height in cm., Apr. 26, 1949	Avg. no. of bolls per plant
7412-30 Exposed	10	25.6	126.1	30.7
7412-30 Control	8	22.8	124.4	22.4
7412-36 Exposed	15	22.1	91.5	10.9
7412-36 Control	16	19.6	78.2	10.1
7412-40 Exposed	15	25.3	135.1	16.3
7412-40 Control	14	27.8	126.9	21.9

TABLE II. Showing certain yield and quality data of exposed and control progeny of certain cotton plants. "Range" = Range measurement.

A—Progeny of plant 7412-30.

Character	Exposed (10 plants) Mean	Range	Controls (7 plants) Mean	Range
Percent lint	32.30	29.9 - 36.3	31.23	29.0 - 34.3
Lint index*	7.06	5.4 - 8.8	7.06	6.2 - 7.7
Boll weight†	1.74	1.2 - 2.1	1.87	1.5 - 2.2
Calculated yield‡	68.39	16.0 - 149.8	51.98	32.0 - 106.1
% 1⅛" + fiber	44.01	25.5 - 65.5	33.29	21.6 - 52.5

B—Progeny of plant 7412-36.

Character	Exposed (8 plants) Mean	Range	Controls (8 plants) Mean	Range
Percent lint	30.82	25.9 - 32.4	32.27	26.7 - 37.4
Lint index	6.10	4.1 - 7.2	6.45	5.5 - 7.2
Boll weight	1.31	0.85 - 1.6	1.74	1.3 - 2.1
Calculated yield	33.44	20.4 - 42.0	41.39	24.2 - 57.4
% 1⅛" + fiber	48.81	22.1 - 77.1	56.66	30.9 - 65.4

C—Progeny of plant 7412-40.

Character	Exposed (9 plants) Mean	Range	Controls (10 plants) Mean	Range
Percent lint	31.27	27.6 - 33.4	31.74	30.0 - 34.6
Lint index	6.86	6.0 - 7.4	6.95	5.9 - 8.3
Boll weight	1.66	1.1 - 2.2	1.61	1.2 - 2.0
Calculated yield	53.73	16.0 - 109.0	47.94	22.0 - 72.0
% 1⅛" + fiber	46.26	28.3 - 74.7	40.70	31.3 - 60.5

*Grams of lint on 100 seed
†Grams of lint per boll
‡Number of bolls × grams of lint per boll

TABLE III. The segregation of green and light green and yellow edge cotyledons in the second generation after exposure. Exp. = "Exposed; Con. = "Control."

Parent plant	Green or light-green cotyledon Total exp.	Total con.	Percentage exp.	Percentage con.	Yellow edge of leaf Total exp.	Total con.	Percentage exp.	Percentage con.
7412-30	558	408	79.4	90.9	145	41	20.6	9.1
7412-36	405	186	67.4	96.9	196	6	32.6	3.1
7412-40	383	599	62.9	92.1	226	51	37.1	7.1

TABLE IV. Showing segregation in exposed and control progenies as to certain seedlings characters.

Parent Plant	Phenotype* I %	II %	III %	IV %	V %	VI %	No. Counted	No. Planted	% Counted
7412-30									
Exposed	52.7	41.1	0.8	2.3	1.4	1.8	2097	3000	69.9
Control	46.5	46.3	1.3	3.3	1.1	1.6	1663	2300	72.3
7412-36									
Exposed	22.7	56.8	4.3	0.5	10.1	5.6	1265	2340	56.6
Control	20.4	59.1	3.5	3.3	4.2	9.4	1367	1840	78.6
7412-40									
Exposed	29.0	56.8	1.2	0.3	7.6	5.8	1763	2789	68.0
Control	46.8	39.4	1.0	0.6	5.9	6.3	2079	3180	70.5

* The characters tabulated are as follows:
I Normal green cotyledon
II Light green cotyledon
III Yellow edged leaf
IV Greenish yellow cotyledon
V Patterned cotyledon
VI Seed hull adhering to cotyledon

In the counts on progeny from 7412-36, an apparently new character was found. This was called "3d leaf" to designate seedlings in which the third developing leaf was very prominent and erect. Of 1194 exposed seedlings 20.1 percent showed "3d leaf." Only 2.8 percent of 1238 controls possessed the character. The other two parent stocks did not show the "3d leaf" character in either control or exposed groups. The significance of this character remains to be finally evaluated.

Discussion

Three aspects of the experimental procedure may be criticized, i.e., the tissues were in resting stage, they were highly heterozygous, and the dosage in terms of roentgen units was small. Rapidly growing tissues are more sensitive than dormant tissues to radiation changes. The heterozygous nature of the test material and the low total radiation dosage increase the difficulty of detecting induced mutations. Future experiments must attempt to increase the time of exposure of a better selected assay organism. The preliminary data outlined in this report do not demonstrate biological changes incident to exposure to all components of cosmic radiation during rocket flights to 90-mile altitudes.

Summary

Samples of seed from individual cotton plants known to be heterozygous for certain seedling defects were exposed to high altitude radiation in an experimental type V-2 rocket. An altitude of 90.5 miles was reached during a 595.5 second flight. The exposed seed were grown through the second generation against controls from the same parent plants. Changes noted in the radiated material remain to be finally evaluated, and cannot as yet be designated as cosmic radiation effects.

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HOW TO BREED A SEX-DIMORPHIC CANARY

Lois in Gene-Wonderland

A canary breeder achieves Utter Genetic Confusion in explaining how to breed a "sex-dimorphic canary." Cafeterias for chromosomes, permanent hybrids, planned mutations, some new gimmicks in sex-linkage, and inhibitors which increase vigor—these do not exhaust the items crammed into these few paragraphs which geneticists will view with incredulous amazement.

"FIRST of all, it is obvious that anyone who is planning to raise dimorphics is well advised to be able to identify both sexes and thus breed a strain that is as "pure" as possible from whatever beginning is made. . . .

"There have been such absurdities advanced as the statements of persons who claim authority, that the appearance of dimorphic cocks is "the same as a frosted apricot"; "the frost is a silver frost"; and, crowning all of the misinformation offered — "influenced by lack of protein in the diet." Even allowing for the general second-handedness of such tidbits, it is apparent to anyone with the slightest real knowledge of the subject that the remarks noted are ridiculous, and not commonsense conclusions from strict record keeping. . . .

"The identity and familiar appearance of any kind of bird, animal, or human being is determined by the arrangement of its inherited chromosomes and the arrangement of the individual genes contained in each pair of chromosomes, which produce appearance characteristics by the ability to select proper nourishment from foods and to cause it to be used to develop the color, shape, size, and other distinguishing points of the species. Other active influences resulting from hereditary mixtures of chromosomes (such as Siskin × Canary) are also present in the body, but not seen. The characteristics which can be seen and bred into habitual inheritance, are called "dominant"; the characteristics which are present but not seen are called "recessive." There are in each creature several *dominant* qualities, each one compensated for by a *recessive* quality, which may be similar or contrary in expression.

"The Black Hooded Red Venezuela Siskin originally introduces the Red Factor into a strain of canaries which thereafter remains

hybridized, possessing all of the Siskin qualities, and all of the canary qualities throughout any number of successive breedings. Even though no further back-cross (to Siskin or hybrid of first three generations) is ever used again, the original qualities bred in the stock remain available in the strain, although any or most of them may be modified as to outward appearance by the accidental or deliberate strengthening of a particular habitual form of dominant inheritance, in the various matings used. . . .

"Listing several phases of appearance may help to demonstrate how apparently unknown characteristics can become dominant and therefore visible in the various young from parent birds which do not themselves exhibit any or all of these phases in their own outward appearance. . . .

" 'DILUTES' or Agates; cinnamon ground birds (RF or not) in which the melanin-inhibitor gene is dominant. . . .

"Dimorphics; in this case the distinctive appearance (described at the beginning of this booklet) is produced by the Siskin pattern influence. The dimorphic pattern can be supplied by either parent or both. However, only one form of primary dominance can be produced in each bird, although the dimorphic form of pattern can be given by the cock to his daughters or by the hen to her sons, as well as the father-son, mother-daughter inheritance. Thus we know that the male character and the female character of dimorphic pattern are both present in each bird, the visible pattern being the sex-dominant one, USUALLY. . . .

"Inhibitors; developed by the chromosomes of Siskin and canary, influencing color ground, and directly governing the digestive use of the various food qualities which produce life, vigor and natural color in birds. The inhibitor of red is inherited from canary ancestry, and has its recessive counterpart in Siskins, as there are other varieties of Siskins including a green and a yellow. The inhibitor of yellow comes from Siskin inheritance and this plus a possible yellow-inhibitor from canary ancestry, is quite likely to be the cause of there being so far no true red canaries. Previous work of experts in the non-Red-Factor field have told us that the complete absence of yellow constitution in canaries results in the embryo not hatching—the dominant yellow-inhibitor bred into canaries, plus a recessive yellow-inhibitor, could very well be fatal by this reasoning. "Recessive whites" would appear to me to be created by action of the yellow-inhibitor of CANARY inheritance, where other cinnamon characteristics assume dominance over the natural green. . . .

The yellow (or green, which is yellow plus black) is not bred out of the birds, but is relegated to an inactive or recessive stage. To maintain the balance established in nature by the dominant recessive characters, the yellow MUST be there, although not seen. It is when the vital balance of opposing characters is disturbed by the actual loss of one of the pairs of selective chromosomes, or by the loss of genes within the chromosomes themselves, that the individual is unable to develop the habitual form. The corrective natural balance of opposing characters in all creatures is so firmly fixed, that men regard as a "freak" any real change. The possibilities of genuine mutation to a true red canary which can live, and reproduce, are so small as to be impossible to achieve by hit and miss breeding, and very unlikely even by use of most careful breeding methods. I quite expect caustic comment from quarters where "red" birds are supposed to be raised, but although we have some very deep soft reddish birds, I have yet to see a TRUE RED, or hear actual proof of there being any true red canaries. . . .

A very important breeding point is an understanding of Color Ground. In all the examples, I refer to the rump area as ground color, since there is presented the most readily comparable area of color in ALL canaries, regardless of such incidentals of general appearance as frost, or lack of it, markings, etc.

—from Lois M. Fristrom,
Breeding Sex-Dimorphic Red Factors

It's perfectly simple: Keep one eye on the rump of the male, the other eye on the digestible action of the chromosomes of the female (if it is a female), block that lethal, and whoops-a-daisy! Ed.

THE NUMBER OF PROGENY REQUIRED TO TEST A MALE FOR HETEROZYGOSITY

For a Recessive Autosomal Gene

JAMES F. KIDWELL
Department of Animal Industry, University of Nevada, Reno

WRIEDT[6] has pointed out that many great sires have proved heterozygous for lethal genes of one type or another. Mead, Gregory and Regan[5] studied recessive genes in dairy bulls selected at random and concluded: ". . . any bull (or cow) selected at random has a good chance to be heterozygous for lethal or other deleterious recessive genes." Lerner[4] has compiled a check list of lethal and sub-lethal mutants in cattle, sheep, horses, swine and poultry, and several new ones have since been reported.[3,1] It is certain that a large number of undesirable recessive genes exist in our livestock and poultry populations.

The frequency of a deleterious, lethal or undesirable allele often becomes high enough in a herd or flock to pose an economic problem. Although in some cases outcrossing would stop the appearance of the undesirable homozygous recessive, the herd or flock has usually been developed to a high degree of productivity and the owner is loath to risk loss of production with an outcross. Gregory, Mead and Regan[2] cite such a case in dairy cattle. It appears that in the future the testing of males as carriers of deleterious recessive genes will assume increasing importance. A knowledge of the minimum number of matings or progeny required to test a male would be useful. Although the necessary facts have long been known, and the solution is elementary, to the best of the author's knowledge, this problem has not been presented in a form generally available to animal husbandmen. It is the purpose of this paper to do so.

Discussion

A prospective sire may be suspected of being heterozygous for a deleterious recessive autosomal gene and it is desired to prove him by a progeny test. Should he sire any homozygous recessive individuals, the evidence is conclusive (barring a mutation) that he is heterozygous. However, he may actually be heterozygous and produce a number of normal test progeny, due to the vagaries of chance. The problem is to determine the minimum number of normal test progeny required to consider a sire homozygous.

An hypothesis, H_o may be formulated and tested: in this instance that the male is heterozygous. If the five percent level of significance is accepted, it is required that if H_o is true, the probability of rejecting it be no greater than .05 or one in twenty. That is, it is required that the probability of deciding the male is homozygous when in fact he is heterozygous be no greater than .05. The only valid decision is to accept H_o if any of the test progeny are homozygous recessive and to reject it if none is recessive.

The statistical problem is to determine the minimum number of births (n) for which the probability of rejecting H_o (i.e., the probability of no homozygous recessive progeny) is .05 or less even though the individual being tested is actually heterozygous. The known rates of mutations in livestock are so low as to be negligible, and are ignored in these calculations.

This probability is simply the binomial for zero occurrances of a homozygous recessive individual in n births, the probability of a homozygous recessive in any one birth being p, which in this particular instance simplifies to the expression $(1\text{-}p)^n$. It is required to find the minimum n for which $(1\text{-}p)^n$ is .05 or less.

There are a number of ways a male can be tested for heterozygosity, depending on the frequency of the recessive allele in the female test group. In general, if the frequency of the recessive allele in the test group is q, and if H_o is true, the probability of a homozygous recessive in any one birth is $q/2$. The general problem is to determine the smallest n for which $(1-q/2)^n \leq .05$. Several of the more feasible test matings with different values of q are considered.

I. *Mating to known heterozygous females*

The value of q is .5, and for n equal to 11 the probability of erroneously rejecting H_o is .0422. Thus, if a male produces 11 normal

progeny from females known to be heterozygous, the chances are 0.958 to 1.000 that he is homozygous normal.

It is not often that such a group of females will be available for test purposes.

II. *Mating to daughters*

It is assumed that the dams were not heterozygous, i.e., if a daughter is heterozygous, the recessive gene must have come from the sire being tested. The value of q is 0.25 and 23 is the minimum value of n. It is not required that all matings be from different daughters.

This method is slow and apt to be costly, especially if inbreeding is undesirable. Further, the male will already have been widely used by the time he is tested. For most species two or more years would be required to complete the test. Mating a sire to known heterozygous females is more than twice as efficient as mating him to his daughters.

If one is willing to accept a 10.3 percent chance of deciding a male is homozygous when in fact he is heterozygous, the minimum number of matings is reduced to 17.

III. *Mating to full sibs*

It may be assumed either that only one or that both parents were heterozygous.

Considering first that both sire and dam were heterozygous and that homozygous recessive individuals do not reproduce, q is equal to 0.333 and the minimum value of n is 17.

If the evidence indicates that only one ancestor was heterozygous, q is equal to 0.25 and minimum n is 23, the same as for sire-daughter matings. This test would be applicable to poultry and possibly to swine, but not to cattle, sheep and horses.

IV. *Mating to half sibs*

If it is assumed that only the common ancestor was heterozygous, q is equal to 0.25 and minimum n is 23, as in sire-daughter matings.

V. *Other tests*

Tests involving relatives more remote than half sibs may be devised, but it is not likely they would be practical for livestock and poultry.

For most recessive genes, the homozygous recessive would either fail to reproduce or be so undesirable that a group of such females would not be maintained. However, there may be instances when such a group would be feasible. For example, if in a population of black cattle the frequency of the gene responsible for red coat color were high, it might be feasible to maintain a small herd of red females to test prospective herd sires. In such a case q is equal to 1 and minimum n is 5.

It is possible that two or more groups of test females are available with different values of q. The product of the probabilities are used in such a case. For example, a breeder might have four females known to be heterozygous and a group of full sibs. The problem is to determine the smallest number of additional full sib matings. For the known heterozygotes q is 0.5 and for the full sibs 0.25. It is required then to find the smallest n for which $(.75)^4\ (.875)^n \leq .05$. The condition is satisfied by n equal to 14.

Summary

The minimum number of progeny required to test a male at the 5 percent level of significance for heterozygosity for a single autosomal recessive gene is calculated for different test matings. These are summarized below.

	Test Mating	Minimum number of progeny
Sire mated to:	Homozygous females	5
	Known heterozygous females	11
	Daughters	23
	Full sibs (one parent heterozygous)	23
	Full sibs (both parents heterozygous)	17
	Half sibs	23

It should be noted that while these tests were devised for a specific gene, the tests are valid for any locus. For example, a male that produces 23 normal and no homozygous recessive progeny from full sib, half sib, or sire daughter matings may be considered a non-carrier of recessive autosomal genes.

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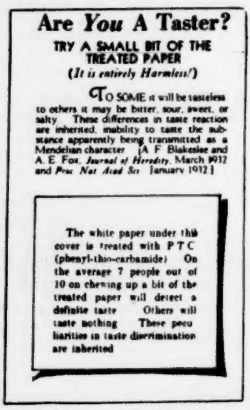
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